Biodiversity and Primary Productivity in Subtropical Forests — Fixing Carbon to Mitigate Climate Change

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I dedicate this thesis to my family.

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Summary

Summary

Forests cover ca. 30% of the world's land surface, store ca. 45% of terrestrial carbon, contribute ca. 50% of terrestrial net primary production and are important in regulating climate, providing food, timber, energy, recreation space and shelter to humans as well as for a myriad of organisms. However, over the last two decades, humans have changed ecosystems more rapidly and extensively than ever, causing a decline in global forest biodiversity at an unprecedented rate. Research in grassland and microbial ecosystems identified a positive relationship between biodiversity and productivity. In contrast, experimental evidence and knowledge about the underlying mechanisms for a relationship between biodiversity and ecosystem functioning (BEF) in highly diverse forests is still lacking. Especially when considering the temporal and spatial scale, large manipulated field experiments offer promising conditions to substantially increase our scientific knowledge about forest ecosystems.

To fill this gap in knowledge, in this thesis I provide insights into the interplay between biodiversity and biomass productivity as well as the production of leaf litter in a large and complex manipulative forest biodiversity experiment (BEF-China) in subtropical south eastern China. The experiment comprises an area of approximately 40 ha, where a total of 226'400 individual trees from 40 species from the local species pool were planted together with shrubs from 20 species. The experimental design features six levels of tree species richness (1, 2, 4, 8, 16 and 24 species) which are partially factorially crossed with four levels of shrub species richness (0, 2, 4, 8 species).

Within the level of primary producers

The first chapter of this thesis provides evidence for a strong positive relationship between woody species biodiversity and forest stand productivity in the experimental forest plots. I assessed stand-level tree productivity through monitoring stem basal area and the tree height of the 16 central tree individuals in 387 plots in September/October over a period of four years (2013–2016) after initial establishment of the experiment in 2008/2009. The results demonstrate that stand-level tree productivity increased with tree species richness. Increasingly positive complementarity effects combined with weakening negative selection effects caused a strengthening of the positive overall net biodiversity effect over time. In addition, the presence of shrubs in the understorey was found to have a negative effect on stand-level tree productivity. Interestingly, this negative effect was attenuated by increasing shrub species richness, indicating that a diverse understorey may positively contribute to ecosystem functioning. The findings of this study furthermore indicate that the reported effects hold true over larger scales, as the results were identical in plots of different sizes.

Across trophic levels

In the second chapter, I further explore the mechanisms causing the positive biodiversity effects with a focus on inter-trophic interactions. Using experimental manipulations of pathogens and herbivores across five diversity levels (1, 2, 4, 8, 16 species), I assessed the relative importance of herbivore and pathogen damage as a mechanism that might drive the observed biodiversity–productivity relationships in subtropical forest. I found that the pathogen-exclusion treatment significantly weakened the positive relationship between woody species richness and tree productivity, a finding that supports the idea that greater leaf pathogen pressure inhibits productivity in low-diversity plots and that in more diverse plots the negative effect of pathogens is less severe. However the effects of the herbivore-exclusion treatment did not change the relationship between tree species richness and stand-level productivity. This implies that in subtropical forests complementarity in enemy niches, in particular for leaf pathogens, enhances biodiversity effects at the community level.

Beyond productivity

In the last two chapters I extend the focus of this thesis to investigate the effects of biodiversity on another important ecosystem function — forest leaf litter production. This is an important ecosystem function because leaf litter constitutes the link between above- and belowground processes through carbon and nutrient cycling.

In the third chapter, I report the results from a study where I set up litter traps across five diversity levels (1, 2, 4, 8, 16) in the BEF-China experiment and determined the monthly amount of litterfall. I found a positive effect of tree species richness on yearly leaf-litter production; this positive relationship increased significantly over time. The overyielding of litterfall was positively correlated with vertical crown complementarity, suggesting a mechanism related to complementary light use, which promotes litter production in species-rich forests. Different tree species showed different temporal dynamics of litterfall, which ensured a more or less constant litter supply in species-rich plots across the whole year. Other research in the BEF-China project demonstrated that diverse leaf litter positively affects mineralization rates; and this might, in turn, enhance stand-level tree productivity.

From the experiment to natural ecosystems

In the fourth chapter, I present results from a similar study where litter traps were installed in comparative study plots in a natural forest located in the vicinity of the experimental site. The litter traps were established along a natural gradient of tree species richness. With the comparative study plots I was able to incorporate other covariate effects (e.g. successional stage) to get a better estimate for the real strength of the effects of species richness under realistic ecosystem conditions, thereby accounting for other factors that might have affected the BEF relationship in the natural forest plots. I found similar positive effects of species richness on litterfall as in the study from the manipulative experiment described in the previous chapter: more diverse forest stands produced more leaf litter. In addition, this litter had higher overall N concentration, which might promote forest growth through accelerated nutrient re-cycling. This study provides strong evidence that mixtures do have higher litter production and demonstrates how this could contribute to the overyielding in subtropical tree growth that was reported for the experimental communities in the first chapter of this thesis. These results highlight the important role of litter-mediated interactions among trees in affecting BEF relationships.

In a nutshell

The present thesis contributes new knowledge to the mechanistic understanding of BEF relationships in subtropical forests. The results highlight the potential of the establishment of mixed-species stands to simultaneously mitigate climate change and enhance biodiversity restoration.

Zusammenfassung

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Wälder bedecken ca. 30% der weltweiten Landfläche. Sie speichern ca. 45% des terrestrischen Kohlenstoffs, sind für knapp 50% der terrestrischen Primärproduktion verantwortlich und spielen eine wichtige Rolle bei der Klimaregulation. Wälder stellen Nahrung, Holz, Energie, Erholungsraum sowie Schutz- und Rückzugsflächen für Menschen und Millionen anderer Arten von Lebewesen zur Verfügung. In den letzten beiden Jahrzehnten veränderten die Menschen diese Ökosysteme stärker, schneller und umfassender als dies jemals zuvor der Fall war. Dadurch verringerte sich die Biodiversität in Waldökosystemen in einem noch nie da gewesenen Ausmass. Forschung auf Graslandflächen und in mikrobiellen Ökosystemen konnten positive Zusammenhänge zwischen der Biodiversität und der Produktivität solcher Systeme belegen. Stichhaltige experimentelle Beweise für vergleichbare Zusammenhänge zwischen der Biodiversität in Waldökosystemen und deren Ökosystemfunktionen (im Englischen „biodiversity–ecosystem functioning (BEF) relationships“) fehlen jedoch bisher. Gerade im räumlich-zeitlichen Kontext solcher Fragestellungen bieten gross angelegte Experimente, welche die Manipulation verschiedener, unter Umständen wichtiger Faktoren erlauben, eine grosse Chance für einen Zugewinn unseres Wissens.

In der vorliegenden Arbeit werden wichtige Zusammenhänge zwischen dem Artenreichtum und dem Biomassezuwachs sowie der Laubstreuproduktion von Baumbeständen im Rahmen eines grossen Waldexperimentes in der subtropischen Region Südostchinas (BEF-China) untersucht. Das Experiment umfasst eine Fläche von knapp 40 ha, auf der 226’400 Einzelbäume aus einem Artenpool von insgesamt 40 Baumarten der lokalen Flora gepflanzt wurden. Das experimentelle Design dieses gross angelegten Versuchs umfasst sechs Stufen des Baumartenreichtums (1, 2, 4, 8, 16 und 24 Arten). Teilweise wurden innerhalb dieser Baumdiversitätsstufen in einem faktoriell-gekreuztem Design auch vier Diversitätsstufen von insgesamt 20 lokalen Straucharten eingepflegt (0, 2, 4 ,8 Straucharten).

Die Stufe der Primärproduzenten

Das Erste Kapitel der vorliegenden Arbeit belegt einen stark positiven Zusammenhang zwischen der Biodiversität der Baumarten und dem Biomassezuwachs der untersuchten Baumbestände auf den Versuchsflächen. Ich erfasste die Produktivität von Baumbeständen durch das Monitoring des Zuwachses der Grundfläche der Stämme sowie des Höhenzuwachses der zentralen 16 Individuen in 387 Versuchsflächen jeweils im September und Oktober über einen Zeitraum von 4 Jahren (2013–2016) nach der ursprünglichen Einrichtung des oben beschriebenen Experimentes in den Jahren 2008 und 2009. Die

Ergebnisse belegen einen Anstieg der Produktivität der Baumbestände mit zunehmender Baumartenzahl.

Komplementaritätseffekte zwischen Baumarten, deren Stärke über die Zeit hinweg zunahm, in Kombination mit einer Abnahme der Stärke von sich negativ auswirkenden Selektionseffekten, verursachten zudem eine Zunahme der Stärke des Biodiversitäts–Produktivitätszusammenhangs mit zunehmendem Alter der Waldbestände. Darüber hinaus zeigten die Ergebnisse dieser Studie, dass die Anwesenheit von Straucharten im Unterholz einen negativen Effekt auf die Zunahme des Biomassevolumens der Baumbestände hatte. Dieser negative Effekt wurde jedoch mit zunehmender Strauchartenzahl schwächer. Dies weist darauf hin, dass ein artenreicher Unterwuchs die Gesamtheit des funktionellen Gefüges eines Waldökosystems festigen kann. Die gefundenen Ergebnisse liessen sich zudem auch auf Flächen verschiedener Grössen übertragen. Dies verdeutlicht, dass die gezeigten BEF-Zusammenhänge auch auf grösserer räumlicher Skala ihre Gültigkeit behalten.

Über trophische Ebenen hinweg

Im zweiten Kapitel untersuchte ich die Mechanismen, die diesem positiven Effekt der Biodiversität zugrunde liegen, mit einem Fokus auf die Interaktionen zwischen verschiedenen trophischen Ebenen. Durch die experimentelle Manipulation von Pathogenen und Herbivoren über fünf Stufen der Baumdiversität hinweg (1, 2, 4, 8 ,16 Baumarten) erfasste ich die relative Wichtigkeit der Schädigung von Bäumen durch Herbivoren bzw. Pathogene, um herauszufinden ob sich hier ein Mechanismus findet, der dem beobachteten Zusammenhang zwischen Biodiversität und Produktivität in subtropischen Wäldern beeinflusst. Meine Beobachtungen zeigten, dass der Ausschluss von Pathogenen den im ersten Kapitel beschriebenen positiven Zusammenhang zwischen Baumartenreichtum und Biomasseproduktion signifikant abschwächt. Dieses Ergebnis bestätigt die Hypothese, dass eine höhere Belastung durch Pathogene die Biomasseproduktion in artenarmen Beständen abschwächt, und dass dieser negative Zusammenhang in artenreichen Beständen weniger stark ausgeprägt ist. Der Ausschluss von Herbivoren hingegen hatte keinen signifikanten Einfluss auf den beobachteten Zusammenhang zwischen Baumartenreichtum und Biomasseproduktion. Diese Ergebnisse bestärken den Befund, dass in subtropischen Waldökosystemen eine Komplementarität zwischen Baumarten in Bezug auf ihre Empfindlichkeit auch Pflanzenschädlinge besteht, die den positiven Zusammenhang zwischen dem Baumartenreichtum und der Bestandsproduktivität der Bäume verstärkt.

Über die Produktivität hinaus

In den beiden abschliessenden Kapiteln erweiterte ich den Fokus dieser Arbeit auf eine weitere Funktion von Waldökosystemen, die Produktion von Laubstreu. Die Produktion von Laubstreu stellt eine bedeutsame Ökosystemfunktion dar, da durch Zersetzungsprozesse und der daraus resultierenden Nährstoffzirkulation eine Verbindung zwischen ober- und unterirdischen Prozessen geschaffen wird.

Im dritten Kapitel werden die Ergebnisse einer Studie dargestellt, in der ich monatlich die Masse an produzierter Laubstreu entlang eines Gradienten von fünf Stufen der Baumdiversität (1, 2, 4, 8, 16) innerhalb des BEF-China Experimentes erfasste. Hier konnte ich einen positiven Zusammenhang zwischen der Masse der jährlich produzierten Laubstreu und dem Baumartenreichtum der untersuchten Versuchsflächen belegen. Dieser positive Zusammenhang nahm über die Zeit hinweg an Stärke signifikant zu. Die beobachtete Mehrproduktion an Laubstreu zeigte zudem einen positiven Zusammenhang mit der vertikalen Komplementarität der Baumkronen. Dies deutet darauf hin, dass der Mechanismus, der dieser Mehrproduktion zugrunde liegt, in einer sich gegenseitig ergänzenden Nutzung von Licht zwischen den Arten liegt. Verschiedene Baumarten zeigten unterschiedliche zeitliche Dynamiken im Laubabwurf, wodurch sich ein mehr oder weniger konstanter Eintrag an Laubstreu in artenreichen Baumbeständen über das ganze Jahr hinweg ergibt. Andere Untersuchungen innerhalb des BEF-China Projektes belegen, dass sich eine artenreiche Laubstreu positiv auf die Mineralisation von Nährstoffen durch Mikroorganismen auswirkt. Somit liegt die Vermutung nahe, dass eine artenreiche Laubstreu sich letztendlich auch positiv auf das Baumwachstum in artenreichen Beständen auswirkt.

Vom Experiment zum natürlichen Ökosystem

Im vierten Kapitel beschreibe ich die Ergebnisse eines ähnlichen Versuches, in dem Laubstreufallen entlang eines Gradienten von Baumdiversität in Vergleichsflächen in einem natürlichen Wald nahe des BEF-China Experimentes ausgebracht wurden. Aufgrund des ähnlichen Designs zur vorherigen Studie ermöglichte es diese Untersuchung abzuschätzen, in welchem Ausmass die Ergebnisse der Studie im experimentellen System auf natürliche Waldsysteme übertragbar sind. Unter Einbeziehung weiterer Effekte, die Einfluss auf die Laubstreuproduktion nehmen könnten (z.B. das Sukzessionsstadium des Waldes), ermöglichte das zugrunde liegende statistische Modell die Ableitung robusterer Schätzwerte für den tatsächlichen Effekt des Baumartenreichtums auf die Laubstreuproduktion in natürlichen Ökosystemen. Ähnlich wie in der vorhergehenden Studie konnte ich einen positiven Zusammenhang zwischen Baumartenreichtum und Laubstreuproduktion aufzeigen. Artenreichere Waldbestände produzierten, aufs Jahr gemessen, höhere Massen an Laubstreu. Darüber hinaus stellte ich fest, dass die Laubstreu artenreicher Bestände insgesamt höhere Konzentrationen an Stickstoff beinhalteten, was möglicherweise dazu führt, dass solche Bestände ein höheres Wachstum aufgrund erhöhter Nährstoffumsatzraten zeigen. Somit legt diese Studie dar, dass artenreichere Wälder eine höhere Produktion an Laubstreu aufweisen, welche wiederum zu der im ersten Kapitel beschriebenen beobachteten Mehrproduktion im Baumwachstum führen könnte. Die Ergebnisse dieser beiden Kapitel meiner Dissertation heben die wichtige Rolle von durch Laubstreu bedingten Interaktionen zwischen Baumarten innerhalb des Gefüges von Biodiversität und Ökosystemfunktionen hervor.

Kurz und Bündig

Die vorliegende Arbeit ergänzt in ihrer Gesamtheit das mechanistische Verständnis über die Zusammenhänge zwischen Baumdiversität und Ökosystemfunktionen subtropischer Wälder um mehrere neue Erkenntnisse. Die gezeigten Ergebnisse verdeutlichen das grosse Potential, das die Errichtung von Mischwäldern sowohl auf die Abschwächung des Klimawandels als auch die Erhaltung der Biodiversität birgt.

Introduction

如果有来生，
要做一棵树，
站成永恒。
没有悲欢的姿势，
一半在尘土里安详，
一半在风里飞扬；
一半洒落荫凉，
一半沐浴阳光。
非常沉默、非常骄傲。
从不依靠、从不寻找……

If there's afterlife,
l would be a tree,
stand in eternal.
no sorrow or happy gesture,
half sleep in dust,
half fly in the wind;
half in shade,
half in sunshine.
very silent, very proud.
never depend on anyone,
never looking for anyone...

三毛 ≪说给自己听≫

Introduction

Ecological and sociological significance of forest ecosystem

Forests cover ca. 30% of the world's land surface (Bonan 2008; Hansen *et al.* 2013), exposing an even more exceptionally large ecosystem volume with their vertical structure from deep in the soil with the extended root system to high up in the canopy with woods and crowns. With stems and crowns, trees in the forests take over the role of ecosystem engineers (Nadrowski *et al.* 2010; Chapin *et al.* 2011), absorb carbon dioxide and store carbon while releasing oxygen into the air — and the amount is extraordinary. Forests store about 45% of terrestrial carbon, contribute about 50% of terrestrial net primary production and can thus sequester large amounts of carbon annually. Carbon uptake by forests contributed 2.4 Pg C year^{-1} to the terrestrial carbon sink from 1990 to 2007, which is comparable to the amount released from fossil fuel emissions and land-use change sources minus ocean and atmospheric sinks (Pan *et al.* 2011). Forests thus contribute extensively to biogeochemical cycles and are of great importance globally in regulating climate (Bonan 2008).

Forests feature high levels of heterogeneity in terms of a diverse microclimate and micro-topography, providing food, timber, energy and recreation space and shelter to humans as well as for a myriad of other organisms (Thompson *et al.* 2011; de Groot *et al.* 2012). Three hundred million people across the globe are living in forests and close to 1.6 billion, more than 25% of the world's population, depend on forest resources for their livelihoods (FAO 2010). Novel writers and film directors living in cities always paint forests as an oasis of freedom that offers a retreat from the depression of civilization. They get inspiration from forests to create valued literature, such as Walden, Epic of Gilgamesh, Harry Potter, Avatar, etc.

Forests harbour a large proportion of global biodiversity — more than two third of all the plants and animals that exist on terrestrial land (FAO 2010), most of them in subtropical and tropical forests. Lots of species living in the forests have not even been discovered yet.

However, as global demand for products like timber, paper, beef and oil continues to rise, forests are cut down (Foley *et al.* 2005; Hansen *et al.* 2013). Over the last two decades, humans have changed ecosystems more rapidly and extensively than ever before; and the conversion of forests to agricultural and pasture land continues at an alarmingly high rate (Foley *et al.* 2005). Biodiversity is declining at an unprecedented rate globally (Butchart *et al.* 2010), reaching a high-risk level according to the planetary-thresholds concept (Rockstrom *et al.* 2009; Steffen *et al.* 2015). Tree and other species are in danger of becoming extinct. Faced with an even accelerating loss of species with anthropogenic activities, will there be lower levels of forest functions and services with fewer tree species?

The answer to these questions stands at the center of the realm of biodiversity and ecosystem functioning (hereafter BEF) research.

Research on biodiversity–ecosystem functioning relationships

In natural ecosystems, species evolved strategies that allow them to coexist in a well-defined dynamic system that keeps up essential functions for a sustainable provision of suitable habitats and nutrients, thus forming a well-functioning ecosystem. The term “biodiversity” is a contracted form of "biological diversity", which has been coined by W.G. Rosen in 1985 while planning the 1986 National Forum on Biological Diversity. It first appeared in a publication in 1988 when E. O. Wilson used it as the title of a proceedings volume (Wilson 1988).

Biodiversity generally refers to the variety and variability of life on Earth, including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems (Capistrano *et al.* 2005).

Currently, invasive alien species, climate change, nutrient loading and pollution, habitat change and overexploitation are major threats to biodiversity. Understanding the relationships between biodiversity and ecosystem functioning is important.

“It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised.”

Darwin & Wallace (1858)

The initial rationale for a link between biodiversity and ecosystem functioning was laid out by Charles Darwin and Alfred Wallace (Darwin & Wallace 1858). Darwin reported from a designed garden experiment to compare the performance of different species and various mixtures of grasses and herbs on different types of soil. Communities composed of organisms developed under “many and widely differing forms” had higher rates of “productivity and decomposition” (Darwin 1859; Hector & Hooper 2002). Darwin explained it with the principle of divergence, which stated that a set of diversified animals can consist of differently skilled and highly proficient specialists. This not only makes them collectively more competitive (relative to other less-diversified and thus less specialized groups), but also better enables them to maximize their use of available resources in any given area (Darwin 1859).

One hundred years after that, MacArthur (1955), as well as Elton (1958) proposed that greater diversity leads to greater ecosystem stability, greater resistance to invasion by exotic species and lower disease incidence. Hutchinson (1959) tried to explain the question of why so many competing species coexiste in nature. May (1973) first presented mathematical theory showing that populations of individual species were less stable at higher biodiversity in model ecosystems, which sparked debate about the effects of biodiversity on stability in real ecosystems. For the second printing of his book (1974), he added an alternative resolution to the debate — that ecosystem properties could be more stable at higher diversity even as population stability was lower. Around twenty years later, this research area was finally established into a scientific, quantitative framework following a conference and edited volume from the conference (Schulze & Mooney 1993). Since then it has become a research front. Results until 2008 have been summarized in the edited volume "*Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective*" (Naeem *et al*. 2009). The metaphor of comparing species' disappearance from Earth to rivets lost from an airplane brought more interests and motivated ecologists to think about how changes in biodiversity affect ecosystem functioning (Ehrlich & Ehrlich 1981).

Comparative studies had often been used to explore BEF relationship. However major progresses related to BEF were obtained with manipulative experiments. Manipulative experiments allow control over environmental factors in such a way that they are similar for different biodiversity levels, an important feature of a study design, because it allows for the identification of mechanisms behind an observation. This is impossible to achieve in comparative studies, because there one can never be sure if biodiversity is a cause for observed effects or if biodiversity is itself influenced by other variables. In manipulative experiments, as the term indicates, different levels of biodiversity are set by the researcher via manipulation of the ecosystem, so that observed differences in ecosystem functioning must be a consequence of the manipulated biodiversity levels. Thus, in manipulative biodiversity experiments, biodiversity can be used as a fixed explanatory variable to explore its effects on dependent random variables related to ecosystem functioning. Therefore, manipulative experiments, with random allocation of biodiversity treatments to plots, keeping environmental conditions similar for each diversity level, are needed to complement comparative BEF studies. Such experimental approaches have successfully been applied during the last decades in the study of the relationship between biodiversity and ecosystem functioning in grasslands (Tilman & Downing 1994; Hector *et al.* 1999; Reich *et al.* 2012), and in terrestrial or aquatic microcosms (Naeem *et al.* 1994; Naeem & Li 1997).

The first published study from a manipulative BEF experiment was from the so-called Ecotron (Naeem *et al.* 1994). In their experiments, Shahid Naeem and his teammates manipulated plant and animal species richness in 14 enclosed terrestrial microcosms, simplified versions of small-scale ecosystems where a variety of environmental variables could be fully controlled. The authors found that more species-diverse communities absorbed more CO_2 and showed a higher overall productivity. In the same year, D. Tilman's group also published an article in Nature about results from a grassland experiment at Cedar Creek, showing that species-rich plots were more resistant to drought than were species-poor ones (Tilman & Downing 1994). Large biodiversity research platforms were built after that, such as the BIODEPTH in 1995 and the Jena Experiment in 2002, and a number of high-impact papers resulting from these experiments demonstrated negative effects of species loss on ecosystem functioning in grassland ecosystems (Hector *et al.* 1999; Tilman *et al.* 2006; Reich *et al.* 2012; Isbell *et al.* 2015).

However, not everything went on smoothly with the BEF research topic. There was a huge debate at that time (Kaiser 2000). The ecologists M. Huston and D. Wardle were two representatives who disagreed with the conclusions that biodiversity generally has positive effects on ecosystem functions such as primary productivity (Huston *et al.* 2000). They argued that factors other than species richness, such as the presence of particular species in diverse communities, might have explained the rise in productivity (Huston 1997). Furthermore, manipulated BEF experiments with randomized species compositions do not necessarily reflect the real situations in natural ecosystems, where species extinction may not be a random process (Wardle 2016). To show a real benefit of biodiversity, these ecologists argued, the plots would have to demonstrate “transgressive overyielding” (Schmid *et al.* 2008) — productivity of diverse communities would have to be greater than that of the single most productive species in monoculture (Huston 1997).

However, those criticisms did not stop the BEF research; on the contrary, ecologists were encouraged to refute the early results from BEF experiments or to conquer the drawbacks with alternative experimental designs and pursue more knowledge about how species richness can influence ecosystem functioning.

Ecologists tried lots of ways to uncover the underlying mechanisms of positive biodiversity effects to convince critics. Most experiments were carried out in grassland, prokaryotic ecosystems or mesocosms. Complementarity effect (CE) and selection effect (SE) are two commonly distinguished components of the observed overall or net biodiversity effect (NE). The CEs can be caused by positive direct interactions of species (facilitation) (Wright *et al.*) or niche-based differences between species. Niche-based complementarity (Turnbull *et al.* 2016) explains that diverse communities can make better use of resources by taking up different resources, including nutrient, water, light, space etc. (Tilman *et al.* 1997; von Felten *et al.* 2009), or can dilute the density of species-specific enemies, such as pathogens or herbivores (Maron *et al.* 2011; Schnitzer & Klironomos 2011). Researchers tried to explain the CEs with higher functional trait dissimilarity (Wagg *et al.* 2017) or higher phylogenetic distances (Venail & Vives 2013). This initially came from Darwin’s principle of divergence (Darwin 1859), which was mentioned above, stating that the evolution of species into different, complementary niches leads to an ecological “division of labour”. An ecosystem with a diverse community of species functions more effectively in terms of resource capture and cycling, and as a consequence, reaches higher levels of productivity. In contrast to CEs, SEs refer to the situation described by Huston (1997) where a more diverse community has higher chances to contain species with the traits that can contribute to overyielding. Thus, if the overyielding highly correlates with species mean traits rather than variation in traits, it may be that SEs are more important than CEs in such a community. A. Hector and M. Loreau used the Price equation from evolutionary genetics to separate NEs into CEs and SEs by a statistical approach — additive partitioning (Loreau & Hector 2001). By applying this method in grassland experiments, researchers found that commonly CEs increase with time, while selection effects remain constant or decrease (Fargione *et al.* 2007; Reich *et al.* 2012).

Further experiments were established to explore which types of niche differences between species may underpin CEs, e.g. different N resources (von Felten *et al.* 2009) or different species-specific enemies (studied by removing these from experimental ecosystems to manipulate the enemy niches; Maron *et al.* 2011; Schnitzer & Klironomos 2011; Seabloom *et al.* 2017). There is evidence showing that different plant species use different resources, e.g. different chemical compounds, or that they obtain them from different places or at different times (von Felten *et al.* 2009). Furthermore, there is evidence that more species-specific enemies (pathogens or herbivores) in monocultures caused more damage, leading to reduced ecosystem functioning. Thus communities from which enemies had been removed showed weaker biodiversity effects (Maron *et al.* 2011; Schnitzer & Klironomos 2011). However, there are also indications that after years of adaptation, plants in monoculture can increase their investments into defense instead of fast growth, which allows them to better tolerate enemies (Zuppinger-Dingley *et al.* 2016). Finally, there are also cases where removal of enemies leads to even steeper BEF relationships (Seabloom *et al.* 2017).

"We have done the easy stuff, working experimentally with herbaceous communities, and have learned a great deal about the diversity/functioning/stability relationship. However, we now must move on to address those ecosystems that control a good portion of the carbon, nutrient and water balances of the earth — the forests."

Harold Mooney (Mooney 2005)

Biodiversity–ecosystem functioning relationships in forests

In forests, trees have long life spans and extend into large vertical canopy spaces, interacting in complicated networks with other trees and organisms at other trophic levels. Confounding factors such as large environmental heterogeneity make it difficult to disentangle biodiversity signals. Underlying mechanisms of BEF relationships in forests may be different from those that have been found in grassland or microbial ecosystems.

Forest biodiversity

Since the start of the eighteenth century, forestry people already started to look at whether species mixtures will contribute to more production. The debate changed over the centuries (Scherer-Lorenzen 2014). In the eighteenth and nineteenth century, there were high demands for wood as the only source of heating energy. Wood was also an important construction material for houses, furniture and ships. Thus the overall forest production was most important. Foresters thought it would be better to plant monocultures, arguing that different species will have stronger competition and be difficult to manage.

After the nineteenth century, fossil fuels replaced wood as energy source. Forest industries started to demand quality of the wood instead of just quantity. However, afforestation with fast-growing species in monoculture dominated until the middle of the century because the first scientific evaluations of long-term silvicultural experiments that were established in the nineteenth century suggested that monospecific stands of trees were often more productive than mixtures, depending on soil conditions.

After the heat of biodiversity protection during the late twentieth century, as well as after concerns about the ecological sustainability of monocultures and their resistance and resilience to environmental change were being raised, people started to realize the value and importance of combing different species in forestry. Matthew J. Kelty and his colleagues pointed out that it is necessary to understand competition and other interactions among species in order to understand mixing effects for better forestry management: "It is not possible to make general statements that mixed-species stands are better or worse than monocultures for all purposes. The nature of interactions among species controls the differences in production and other ecological processes..." (Kelty & Cameron 1995).

At the beginning of the twenty-first century, people started to realize that diverse natural forests may provide valuable ecosystem services (regulation, culture and supporting services) beyond the one of providing wood as raw material (Gamfeldt *et al.* 2013). However, a systematic and scientific evaluation about the role of forest biodiversity has started only recently.

Comparative studies

During the last two decades, a number of comparative observational studies with a focus on the relationships between biodiversity and productivity were carried out, especially in temperate and boreal forest ecosystems. In 2011, Paquette & Messier were the first to demonstrate a strong positive biodiversity effect on tree productivity considering climate and environmental factors from a large-scale study, using a structural equation model (Paquette & Messier 2011). Analysing data from 12,000 permanent forest plots in Canada, they showed that complementarity (beneficial interactions between species) may be less important in temperate forests with good conditions, whereas in the more stressful environments of boreal forests it may be of higher importance. Consistently, Jucker found that climate modulates the effects of tree diversity on forest productivity (Jucker *et al.* 2016). The influence of tree diversity on wood production was only strongly positive at sites where climate was harsh for wood production and tree packing densities were low, but were weakly negative at sites where climatic conditions for growth were suitable. Chisholm found that the BEF relationships in forests are scale-dependent, with positive relationships found in small spatial grains (0.04 ha) and inconsistent results but more negative relationships found at larger spatial grains (0.25 ha, 1 ha) (Chisholm *et al.* 2013). Some studies in subtropical forests found that tree diversity enhances stand tree growth and carbon storage but not leaf area (Baruffol *et al.* 2013; Castro-Izaguirre *et al.* 2016)

Zhang *et al.* (2012) carried out a first global meta-analysis and demonstrated the critical role of species evenness, species richness and trait variation in defining net biodiversity effects in forest polycultures. There meta-analysis, however, was only based on 54 studies to detect forest biodiversity–productivity relationships in forest ecosystems. Liang *et al.* (2016) analysed data from 777,126 permanent plots, spanning 44 countries globally. They reported a globally consistent positive biodiversity–productivity relationship and highlighted the potential benefits that could arise from the transition of monocultures to mixed-species plantations in forestry practices. Nevertheless, a strong, more mechanistic proof for these relationships is lacking in forest ecosystems. Such evidence may, however, be deducted from manipulative experiments.

Manipulative experiments

Almost all the forest biodiversity experiments are in the TreeDivNet, which can be seen from Table 1 (Verheyen *et al.* 2016). The first forest experiment was set up by J. Koricheva in Satakunta, Finland, in 1999, and has four biodiversity levels of 1, 2, 3 or 4 species (Vehviläinen & Koricheva 2006). This experiment focuses on browsing patterns of voles and moose, testing whether herbivory is reduced in plant communities composed of several different species compared with species-poor or monocultures. The presence and abundance of particular tree species (such as birch, which is preferred by moose) and the population dynamics of voles strongly influenced the observed patterns in herbivory.

More temperate forest experiments were set up after 2003 (Table 1). The largest one in terms of area is BIOTREE, which was established in 2003 in Germany. There is another new network IDENT, which combines two continents, four countries and six cities, including a Mediterranean site in Italy. It focuses on testing for a key role for species' functional traits by replicating high-density tree plots of fixed species-richness levels with variation in functional diversity (Tobner *et al.* 2014; Tobner *et al.* 2016). Recently published results from these experiments in America (Grossman *et al.* 2017) and Belgium (Van de Peer *et al.* 2017) show clear positive overyielding effects of species mixtures.

These experiments are carried out in small plots and with high planting density to observe effects of early interactions among tree seedlings.

In tropical forests, the Sardinilla forest BEF experiment in Panama was one of the earliest. This experiment used three biodiversity levels (1, 3 or 6 species) and observed effects of biodiversity on tree biomass and growth as well as carbon storage and nutrient cycling (Healy *et al.* 2008; Potvin & Gotelli 2008; Zeugin *et al.* 2010; Potvin *et al.* 2011; Ruiz-Jaen & Potvin 2011). Many processes showed a unimodal relationship with highest performance at the intermediate three-species level, and a slight decrease at the six-species level (Potvin & Gotelli 2008; Potvin & Dutilleul 2009).

At about the same time, a tropical forest BEF experiment with 4-ha plots was set up in Sabah, Borneo with the aim to restore tropical forest structure by using enrichment planting of dipterocarps (Hector *et al.* 2011). Using a pool of 16 species, they were planted as single species or mixtures of four and all 16 species under a young tree canopy that provides shade protection. Survival and growth data over the first decade have been recently published (Tuck *et al.* 2016).

The largest forest BEF experiment was set up in subtropical China, using several species pools of 16 tree species, which were used to construct “nested” communities of reduced biodiversity with 8, 4, 2 or 1 species per plot (Bruelheide *et al.* 2014). Trees in the BEF-China experiment were planted in 2009 and 2010 in Xingangshan, Jiangxi Province. It consists of 566 plots on ca. 40 ha of hilly terrain. There are several novel features in the design of the BEF-China experiment. It factorially combines tree species richness levels with shrub species richness, which was allowed to explore interactions in different vertical structures. BEF-China also includes two plot sizes (0.067 ha and 0.27 ha) to make it possible to test effects of spatial scale on BEF relationships. The use of a so-called broken-stick design (see Methods in Chapter 1) to produce species compositions guarantees that every species occurs the same number of times at each species-richness level and allows pairwise analysis. Analysis of each species population performance in different diversity levels can help to better understand mechanisms underpinning BEF relationships.

In summary, forest biodiversity experiments have only recently been set up and the first publications are from specialist studies involving tree seedlings planted at high density, in small plots and at low species richness levels (Potvin & Gotelli 2008; Sapijanskas *et al.* 2014; Tobner *et al.* 2016; Grossman *et al.* 2017; Laforest-Lapointe *et al.* 2017; Van de Peer *et al.* 2017; Williams *et al.* 2017). Most of the forest BEF experiments are located in boreal or temperate forests, neglecting the high species richness of subtropical and tropical forests (Clarke *et al.* 2017). There is a lack of evidence to show effects on large plots with higher diversity levels including larger species pools. For example, we do not know if in highly diverse forests species richness is linearly related to ecosystem functioning or if there will be redundant species that cause a flattening of the relationship at higher biodiversity levels. We also do not know if biodiversity effects in forests are more influenced by species complementarity (CEs) or competitive hierarchies (SEs) or how functional diversity and phylogenetic diversity contribute to biodiversity effects. Further questions are: how do biodiversity effects change with time and scale? What is the role of multi-trophic interactions in BEF relationships? Can manipulative experiments be linked to comparative studies from natural forests? How can we better manage forest ecosystems? The present thesis contributes towards closing some of these gaps in our present knowledge on BEF relationships using the BEF-China experiment.

Objectives of this thesis

In the first chapter, I tested the overall biodiversity–productivity relationships in the BEF-China experiment (Bruelheide *et al.* 2014). There are many measures of biodiversity. Here I used tree species richness (the number of tree species in a given area), as well as taking into account the effect of shrub species richness on stand-level tree growth. Phylogenetic diversity (phylogenetic distances) and functional diversity (species traits distances) were calculated to help to explore underpinning mechanisms. Net biodiversity effects (NEs) were separated into complementarity (CEs) and selection effects (SEs) by an additive partitioning method (Loreau & Hector 2001). Biodiversity effects were tested to explore whether they changed with time and spatial scale. Further mechanisms causing CEs and SEs were detected.

In the second chapter, I dig deeper to study the influence of multi-trophic interactions on BEF mechanisms with a manipulative experiment in order to further explore the enemies-based niche-complementarity mechanism. I excluded the leaf herbivore and leaf pathogen load, respectively, and compared these treatments with control plots. I hypothesized that leaf herbivores and leaf pathogens cause more damage in monocultures, while mixture plantations can buffer these damages by dilution effects from different species, which cause the positive biodiversity effects.

After having demonstrated that plant primary productivity increases with the diversity of plant species, I wanted to know how tree species richness affects litter fluxes — the links between above- and belowground processes through the decomposition of organic material. The production and subsequent turnover of aboveground litter is an important process in the turnover of carbon in ecosystems. In the third chapter, I used the BEF-China experiment to study the relationship between tree species richness and litter production. My hypothesis was that more diverse forest communities produce more litter than less diverse forest communities. In the fourth chapter I explore this biodiversity–litterfall relationship in a comparative study in nearby natural forest. With this I could see whether the results from the manipulative field experiment were similar to those from the comparative study in the natural forest.

Finally, I carried out a social questionnaire survey to bridge science with policy, which can help to promote diverse species plantation in forest management practice. The results of this study are briefly shown in the appendix.

Table 1 Forest biodiversity experiments. Table revised from TreeDiNet (http://www.treedivnet.ugent.be/). The different biodiversity variables studied are: species richness (SR), functional diversity (FD), genetic diversity (GD), phylogenetic diversity (PD), and evenness (EV).

Ecoregion	**Experiment**	**Plant year**	**Sites**	**Plots**	**Plot size (m^2)**	**Diversity**	
Boreal	Satakunta	1999	4	163	400	SR	1,2,3,5 sp.
						GD	1,2,4,8 clones (*Betula*)
Boreal	Satakunta	1999	4	163	400		
Temperate	BIOTREE	2003, 2004	4	117	300–12000	SR	1,2,3,4,6,10 sp.
	BIOTREE					FD	very low - very high
Temperate		2003, 2004	4	117	300–12000		
						EV	
Temperate	BangorDIVERSE	2004	1	92	45-196		
						SR	1,2,3 sp.
	BangorDIVERSE					FD	shade tolerance
Temperate		2004	1	92	45-196		
Temperate		2005	1	98	25		
	Kreinitz					SR	0,1,2,3,5,6 sp.
Temperate	Kreinitz	2005	1	98	25	FD	decomposition rate
Temperate	ORPHEE	2008	1	256	400	SR	1,2,3,4,5 sp.
	ORPHEE					FD	deciduous, evergreen
Temperate		2008	1	256	400		
Temperate	Communitree	2009	1	90	0.24		
						GD	1,2,3,4 half-sib families
Mediteranean	Ridgefield	2010	1	124	447	SR	0,1,2,4,8 sp.
Mediteranean						FD	0,1,2,3,4 levels
	Ridgefield	2010	1	124	447		
Temperate/ Mediteranean	IDENT	2009–2014	6	1640	10.24–20.25		
						SR	1,2,4,6,12 sp.
						FD	3,8 levels
Temperate/ Mediteranean	IDENT	2009–2014	6	1640	10.24–20.25		
	FORBIO	2010, 2012	3	127	1296, 1575, 1764		
Temperate						SR	1,2,3,4 sp.
	FORBIO				1296, 1575, 1764	GD	1,3 provenances (*Quercus*, *Fagus*)
Temperate		2010, 2012	3	127			
Temperate	Climate Match	2011	2	177	144, 1152	SR	1,4 sp.
Temperate	Climate	2011	2	177	144, 1152	GD	1,2,3,4 provenances

Temperate	Match	2012	1	182	60		
	SIDE					SR	0,3,5,7,9 sp.
Temperate	SIDE	2012	1	182	60	EV	even, dominant
Temperate	BiodiversiTREE	2013	1	75	1225	SR	1, 4, 12 sp.
						FD	AM, EM fungi
Temperate	BiodiversiTREE	2013	1	75	1225	GD	1,2 provenances
Temperate	B-Tree	2013	1	44	170–300	SR	1,2,4 sp.
						FD	AM, EM fungi
Temperate	B-Tree	2013	1	44	170–300		
	EFForTS-BEE	2013	1	56	25–1600	SR	0,1,2,3,6 sp.
Temperate	ECOLINK-Salix	2014	3	99	92.16	GD	1,2,3,4 varieties
Temperate	HighDiv-SRC	2015	1	45	92	SR	1,2,3,4 sp.
Temperate	MyDiv	2015	1	80	121	SR	0,2,4 sp.
						FD	AM, EM fungi
Temperate	MyDiv	2015	1	80	121		
Temperate	TWIG-Ugent	2017	1	22	774	SR	1,2,3 sp.
						FD	AM, EM fungi
Temperate	TWIG-Ugent	2017	1	22	774		
Subtropical	BEF-China	2009, 2010	2	566	667	SR	0,1,2,4,8,16 tree + 0,4,8,16 shrub sp.
						FD	SLA & rarity
Subtropical	BEF-China	2009, 2010	2	566	667		
Tropical	Sardinilla	2001, 2003	2	32	675–2025	GD	3-38 half-sib + 1,4 seed families
						SR	1, 3, 6/1,3,6,9,18 sp.
Tropical	Sardinilla	2001, 2003	2	32	675–2025	FD	shade tolerance
Tropical	Gazi Bay	2004	1	32	36	SR	1,2,3 sp. (mangroves)
Tropical	Agua Salud	2008	1	267	1755	SR	1,2,5,6 sp.
Tropical	Sabah	2010	1	124	40000	SR	1,4,16 sp.
						FD	2,3 height classes
Tropical	Sabah	2010	1	124	40000	GD	2,4 genera
Tropical	UADY	2011	1	74	441		
						SR	1,4 sp.
Tropical	UADY	2011	1	74	441	GD	1,4 genotypes (*Swietenia*)
Tropical	BrazilDry	2016	1	155	104	SR	1,2,4,8,16 sp.

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Chapter 1

Strong positive biodiversity–productivity relationships in a subtropical forest experiment

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Strong positive biodiversity–productivity relationships in a subtropical forest experiment

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Forest ecosystems contribute substantially to global terrestrial primary productivity and climate regulation, but, in contrast to grasslands, experimental evidence for a positive biodiversity–productivity relationship in highly diverse forests is still lacking[1]. Here, we provide such evidence from a large forest biodiversity experiment with a novel design[2] in subtropical China. Productivity (stand-level tree basal area, aboveground volume and carbon and their annual increment) increased linearly with the logarithm of tree species richness. Additive partitioning[3] showed that increasing positive complementarity effects combined with weakening negative selection effects caused a strengthening of the relationship over time. In 2-species mixed stands, complementarity effects increased with functional distance and selection effects with vertical crown dissimilarity between species. Understorey shrubs reduced stand-level tree productivity, but this effect of competition was attenuated by shrub species richness, indicating that a diverse understorey may facilitate overall ecosystem functioning. Identical biodiversity–productivity relationships were found in plots of different size, suggesting that extrapolation to larger scales is possible. Our results highlight the potential of multi-species afforestation strategies to simultaneously contribute to mitigation of climate change and biodiversity restoration.

Forest ecosystems harbour around two thirds of all terrestrial plant species, but currently lose biodiversity at high rates which may threaten the production of timber, fiber, fuel and other services beneficial to humans[4]. Observational studies suggest that species-rich forests exceed the productivity of less diverse forests[5,6], but co-varying factors (e.g. spatial heterogeneity in abiotic environment, species composition and successional stages; interventions by forest management) make assigning causation difficult. Systematic experimental manipulations of plant species composition in grassland communities[7-9] have demonstrated that plant diversity promotes community productivity. This effect has been attributed to positive effects of niche partitioning between species, specifically to complementarity in the use of abiotic resources[10] or interactions with enemies[11], or to an increasing contribution of highly productive species in more diverse communities[12]. These two types of mechanisms have been related to statistical complementarity and selection effects obtained by additive partitioning[3]. However, these mechanisms may differ in species-rich forests in which neutral processes may be important[13,14] and where "diffuse" coevolution may result in niche convergence toward generalist strategies[15]. Furthermore, trees have large and persistent vertical structures that support the long-term accumulation of biomass. Several forest experiments have recently been initiated[16,17], but these are mainly in the temperate zone or implemented in small plots with a limited species richness gradients[18-23]. To close these critical gaps in knowledge[1], controlled experiments in which the diversity of tree species is systematically manipulated are needed. The largest such study concerning numbers of treatments and plots has been established in 2009/2010 in subtropical south-east China and is referred to as the BEF-China experiment[2].

Here, we report how stand-level productivity in the BEF-China experiment 3–7 years after planting was related to species richness and how variation within species-richness levels was related to trait differences among species. Experimental forest communities were constructed systematically from a pool of 40 tree (Extended Data Table 1) and 20 shrub species, and were established in plots at two hilly sites (in 2009 at site A and in 2010 at site B). By the time of our later measurements the tree communities were well established with some canopies exceeding 12 m in height in 2016. The design of previous biodiversity experiments had been criticised because not all species were found at all diversity levels, and because the compositions of the experimental communities that were realized were not nested as would be expected with sequential extinction[24]. We adopted a novel design that avoided these caveats[2] (see Methods, Extended Data Fig. 1, Extended Data Table 2). In brief, we first created three pools of 16 species per site. These were then repeatedly split into halves, resulting in nested, non-overlapping subsets of 8, 4, 2 and 1 species. We used these sets, and in addition also the full sets of 24 species per site, to plant tree communities comprising 1 to 24 species. We further established plots with two sizes: 0.067 ha (equivalent to the Chinese area unit of 1 mu; 400 individual trees) and 0.267 ha (4 mu; 1600 individuals). The larger plots were established for one of the three 16-species pools at each site and included a split-plot treatment that consisted of understorey shrubs planted in the center of the quadrats formed by four neighbouring trees. Shrubs were planted at a species richness of 0 (no shrubs), 2, 4 or 8, in factorial combination with the tree species-richness treatment. We assessed stand-level tree productivity in all 1-mu plots (including all 1-mu subplots of the larger plots) non-destructively by measuring stem basal area and height of the 16 central trees every year from 2013–2016 in September/October. We used these data, together with data from separately harvested trees to obtain conversion factors, to calculate tree volume and aggregated the individual volume data of live trees to the stand level. To characterize annual stand growth, we further derived yearly increments of stand volume from successive inventories. Using the same method, we determined the same metrics at the population-level (stand-level data separated into species).

We found significantly positive effects of the logarithm of tree species richness on both stand volume and annual stand volume increment of trees ($F_{1,89} = 5.26$, $P = 0.024$ and $F_{1,94} = 9.34$, $P = 0.003$, respectively; Fig. 1 and Extended Data Fig. 2, Table 1). The size of these effects increased over time ($F_{1,95} = 10.83$, $P = 0.001$ and $F_{1,95} = 12.01$, $P < 0.001$, respectively, for interaction species richness × year). Similar results were obtained for stand basal area and its increment (Extended Data Fig. 3, Table 1). In 2016, at the end of our measuring period, stand basal area increased on average by 1.65 m^2 ha^{-1} and stand volume by 5.09 m^3 ha^{-1} with each doubling of tree species richness. After seven years of growth, the average 16-species mixture stored 22.0 ± 4.5 Mg C ha^{-1} above ground, which is double the amount found in monocultures (9.4 ± 1.1 Mg ha^{-1}, Extended Data Fig. 4) and similar to the productivity of monocultures of commercial plantation species *Cunninghamia lanceolata* (22.4 ± 10.7 Mg C ha^{-1}) and *Pinus massoniana* (21.0 ± 3.0 Mg C ha^{-1}) that we had planted for reference at the same site (Extended Data Fig. 4, Extended Data Table 4). System-level C sequestration likely is higher, given that additional C will have been allocated to belowground tree organs[25] and in part transferred to persistent soil pools important for long-term carbon sequestration. These strong positive effects of tree species richness were driven by faster growth of live trees in more diverse stands, and were unrelated to tree survival rate, which was independent of species richness; if anything, there was a trend towards lower survival at higher richness (Extended Data Fig. 5).

The net biodiversity effect[26] on productivity increased through time for mixtures of all species-richness levels (Fig. 2, $F_{1,48} = 23.61$, $P < 0.001$). The positive effects of tree species richness on productivity were also reflected in a higher frequency of mixtures that overyielded relative to the ones that underyielded and in many cases of transgressive overyielding[26] (Extended Data Table 5). Additive partitioning revealed that the increases of net biodiversity effects were primarily driven by increases in complementarity effects (Extended Data Table 6, $F_{1,31} = 9.61$, $P = 0.004$) and weakening negative selection effects (Extended Data Table 6, $F_{1,37} = 4.61$, $P = 0.038$). In the last year of measurements, selection effects were no longer significantly different from zero (Fig. 2, $F_{1,31} = 3.40$, $P = 0.075$).

We observed considerable variation in overyielding among communities of the same species-richness level. Some of this variation was explained by functional diversity but phylogenetic diversity had low explanatory power. For the 48 different 2-species mixtures, complementarity effects were positively correlated with the functional distance and selection effects with vertical crown dissimilarity, also referred to as crown complementarity between species (Fig. 3, Extended Data Table 7). That vertical crown complementarity[22] contributed to overyielding via selection rather than complementarity effects indicated that it was due to asymmetric light competition[27] and is consistent with the "competition-trait hierarchy hypothesis"[28].

Species with high monoculture productivity (Fig. 4a) explained large amounts of variation in stand-level productivity (Fig. 4b), but their contribution was not always positive, as demonstrated by several negative species-level selection effects (Fig. 4c). Despite the positive effect of species richness on community productivity, the population-level responses of each species to species richness varied from positive to neutral to negative (Fig. 4d). These responses did not differ between evergreen and deciduous species (Fig. 4d, $F_{1,159} = 0.89$, $P = 0.347$). A similar decoupling between community- and population-level responses has previously been reported from grassland biodiversity experiments[8] and indicates that a few positive population-level responses can overcompensate a larger number of negative population-level responses. Nevertheless, the number of species with positive responses to community diversity and the magnitude of their responses increased with time (Fig. 4d).

Competition by understorey shrubs planted in the gaps between the trees reduced stand-level tree volume (Extended Data Table 8, $F_{1,234} = 4.80$, $P = 0.029$), but this effect decreased with shrub species richness (Extended Data Table 8, $F_{1,199} = 5.40$, $P = 0.022$) and was negligible when mixtures of 8 shrub species were planted (Extended Data Fig. 6), indicating reduced competition between shrubs and trees at higher shrub diversity levels. The diversity–productivity relationships we found were scale-independent, i.e. they did not differ between 1- and 4-mu plots (Extended Data Table 8, $F_{1,114} = 0.20$, $P = 0.694$ for interaction species richness × plot size).

Our results provide strong evidence for a positive effect of tree species richness on tree productivity at stand-level in establishing subtropical forest ecosystems, and support the idea that highly diverse subtropical forest ecosystems are niche-structured[22,27]. Seven-year old mixed-species stands can produce an estimated additional aboveground wood volume of 25 m^3 ha^{-1} relative to the average monoculture, which translates to the sequestration of approximately an extra 10 Mg C ha^{-1} (Fig. 1, Extended Data Fig.4). We expect this effect to grow further, given that we did not observed any signs of a deceleration over the present measurement period. The size of the biodiversity effects we found for these forests is similar to biodiversity effects reported from grassland studies[8,9]. Given that plant biomass is higher in forests, and that the largest fraction of tree carbon is bound in relatively persistent woody biomass, these effects translate into significant diversity-mediated rates of carbon sequestration. Substantial forest areas are managed world-wide, with large afforestation programs underway in many countries. In China, huge economic efforts are made for afforestation, with a net growth of total forested area by 1.5×10^6 ha yr^{-1} achieved from 2010 to 2015[29]. However, the overwhelming fraction of newly established forests are monoculture plantations of species with highest productivity in the short term[30]. Our analysis suggests that a similar productivity could be achieved with mixed plantations of native species, which would result in co-benefits in the form of biodiversity management and a likely higher level and stability of ecosystem services in the longer term.

Online content Methods, along with additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Extended Data are available in the online version of the paper.

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Author contributions HB, KM and BS conceived the project with help from all co-authors; YH carried out the measurements; YH, YC, KM, PAN and BS led the data analysis and interpretation. All authors contributed to the writing of the manuscript.

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METHODS

Study site and experimental design

The BEF-China experimental platform was established in Jiangxi Province, China (29°08′–29°11′N, 117°90′–117°93′E). Climate at the site is subtropical, with mean annual temperature and precipitation of 16.7°C and 1800 mm, respectively (averaged from 1971–2000)[31]. A large-scale tree biodiversity experiment was established in 2009–2010 on two sites (A and B) of approximately 20 ha each, with a total of 226’400 individual trees planted. Here, we use all plots in which random species-loss scenarios were simulated. The species pool contains 40 tree species (Extended Data Table 1), 24 for each site (of which eight are shared between sites). The 24 species at each site were divided into three 8-species sets. By combing these 8-species sets in all possible ways, three pools of 16 species were created. The species in each 16-species pool were put in random sequence and then repeatedly divided in halves until monocultures were obtained. This procedure resulted in 70 unique species compositions per site (Extended Data Table 2) and ensured that each tree species occurred in equal overall proportion at each diversity level. We further included monoculture plots with two commercially important tree species, *Pinus massoniana* and *Cunninghamia lanceolata*, as reference, with 5 replicate plots per species and site. Each plot was 25.8 × 25.8 m in size and planted with 400 tree individuals arranged on a rectangular 20 × 20 grid with 1.29 m spacing between rows and columns. To minimize edge effects, plots were established adjacent to each other, with trees thus forming a continuous cover across the entire site. Site A was planted in 2009, site B in 2010.

Plots of one species pool per site (pools A1 and B1 at sites A and B, respectively, Extended Table 2) were additionally replicated in plots that were four times larger and thus contained 1600 trees. These large plots were subdivided into four quadrants in which a factorial understorey shrub-diversity treatment was established. These four subplots either had no shrub understorey (0 species), or shrubs planted in all the centers between 4 adjacent trees, at a diversity of 2, 4 or 8 shrub species (Fig. 1a).

The design we use here consisted of 140 small plots (1 mu) and 64 large plots (4 mu). Out of this total of 396 1-mu sized (sub)plots, nine had to be excluded because these were not established due to a lack of sapling material or high initial mortality. All plots were weeded annually to remove emerging herbs and woody species that were not part of the planting design.

Tree measurements

We assessed stand-level and population-level tree growth by measuring the height of trees and maximum and minimum stem diameter at 5 cm above ground to calculate basal area.

We focused on the central 4 × 4 =16 trees of each 1-mu (sub)plot to avoid edge effects. These measurements were repeated annually in September/October from 2013 to 2016. We aggregated these tree-level data at the species (i.e. population) and stand level.

We further calculated a cylindrical tree volume as the product of basal area and height. The true volume was then obtained by multiplying this proxy with a form factor determined by a complete harvest of 154 trees in natural forest near the experimental sites. The total volume of each harvested trees was calculated as ratio of total aboveground dry biomass and average wood density. Similarly, tree biomass was determined by multiplying the cylindrical volume of each experimental tree with a biomass conversion factor determined based on the harvested trees (Extended Data). Biomass was converted to carbon content[32] by multiplying with 0.474 g C g^{-1}.

Complementarity effect and selection effect

We used the additive partitioning method of Loreau & Hector[3] to decompose net biodiversity effects (NEs) of productivity measures into complementarity (CEs) and selection effects (SEs), separately for each year and diversity level. CEs and SEs depend on relative yields of species, which we calculated using monoculture biomass as denominator. If a species failed to establish in monoculture (which was the case for *Meliosma flexuosa*, *Castanopsis eyrei* and *Machilus grijsii*), or had a mortality exceeding 80% (*Quercus phillyreoides*, *Phoebe bournei*), it was excluded from the set of target species in the corresponding mixtures[33]. Formally, CEs and SEs are related to (co)variances and therefore were square-root transformed with sign reconstruction ($\mathrm{sign}(y)\sqrt{|y|}$) prior to analysis, which improved the normality of residuals[3].

Overyielding and underyielding

Overyielding describes the case where the productivity of a mixture exceeds the average productivity of monocultures of component trees[26]. Conversely, underyielding identifies a lower yield of the mixture relative to monocultures. Transgressive overyielding indicates that the productivity of a mixture exceeds the productivity of the monoculture of the most productive component species. Transgressive underyielding is defined similarly. We determined overyielding and underyielding of all mixtures relative to monocultures. Capitalizing on the nested nature of our design, we further determined the same metrics using the two mixtures with half the set of species as reference, instead of monocultures, i.e. we tested whether combining communities with two sets of species resulted in a community that produced more or less biomass than expected on the assumption of no interactions among the sets (overyielding) or that community productivity would be determined by the more productive set of species alone (transgressive overyielding).

Vertical crown complementarity

We quantified the interspecific complementarity in vertical crown extent of trees in 2016. The crown extent was determined as interval between the lowest side-branch and the top of a tree in monocultures. These data were averaged across all surviving trees of the 16 central individuals planted in a plot. We then calculated vertical crown complementarity in 2-species mixtures as proportional dissimilarity of the crown extents between the two species:

$$PDS_{A,B}=\frac{x_{A\setminus B}+x_{B\setminus A}}{x_{A\cup B}}$$

where $x_{A\setminus B}$ indicates the vertical extent (in meters) that is occupied by A but not by B (vice versa for $x_{B\setminus A}$), and $x_{A\cup B}$ indicates the extent occupied by at least one of the species. This index is equivalent to one minus the proportional similarity index proposed by Colwell and Futuyma[34].

Statistical analysis

We used analysis of variance based on type-I sum of squares linear mixed-effects models to assess the effects of tree species richness (and additional design variables) on productivity[35]. All analyses were done in R 3.3.2 and ASReml-R[36]. The models included the fixed effects site, tree species richness ($\log_2$-transformed), year (continuous variable, centered over our observation period), the interaction $\log_2$(tree species richness) × year, and the interaction site × year. Random effects were species composition (with a separate variance component for each site), plot (with a separate variance component for each site), subplot, and the interactions of all these random terms with year. Model residuals were checked for normality and homogeneity of variances.

For the analyses of shrub diversity effects, the model contained the additional fixed effects shrub presence (a two-level factor: 0 vs. 2, 4 or 8 shrub species), plot size (a two-level factor: 1 vs. 4 mu), $\log_2$ of shrub species richness (for shrub-species richness >0), and the interactions of all these terms with $\log_2$(tree species richness) and with year. Random effects were species composition (with a separate variance component for each site), plot (with a separate variance component for each site), subplot, and the interactions of all these random terms with year (Extended Data Table 6). The interaction of year and site and the site-specific variance terms estimated for some random terms accounted for the fact that site B was established one year after site A and that trees at site B were therefore smaller.

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Data availability statement

The data supporting the findings of this study will be deposited in Pangaea.

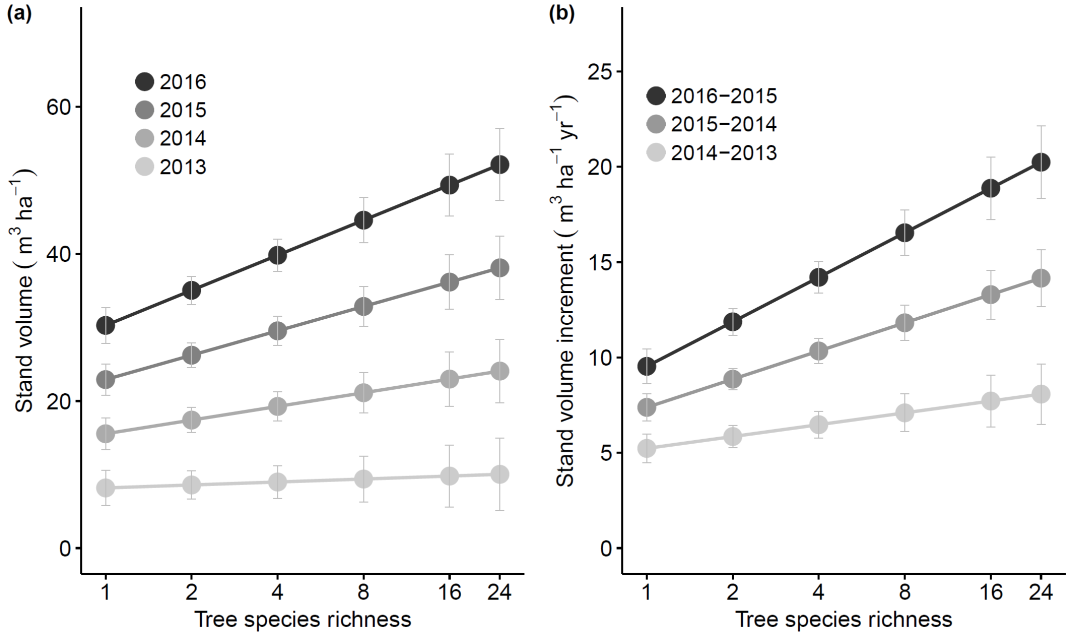


Figure 1 | Stand-level tree volume (a), and its annual increment (b) as a function of tree species richness from 2013–2016. The figure shows predicted means and standard errors based on fitted mixed models (Table 1). Effects of species richness were significantly positive and increased significantly throughout the observation period.

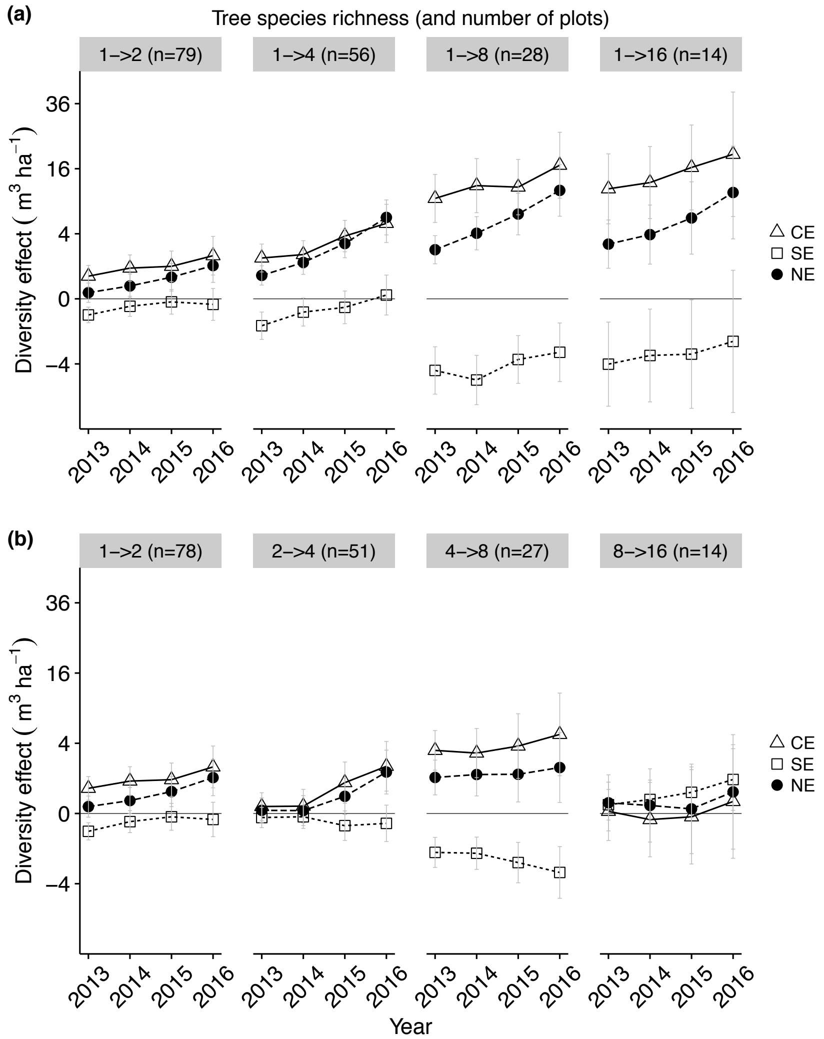


Figure 2 | Changes over time in the net biodiversity effect (NE) and its additive components, complementarity effect (CE) and selection effect (SE), on stand-level tree volume. The figure shows means and standard errors. In (a), diversity effects were calculated with monocultures as reference (Extended Data Table 6), in (b) with component mixtures of half the number of species as reference. The y-axes are square-root scaled to reflect the quadratic nature of biodiversity effects.

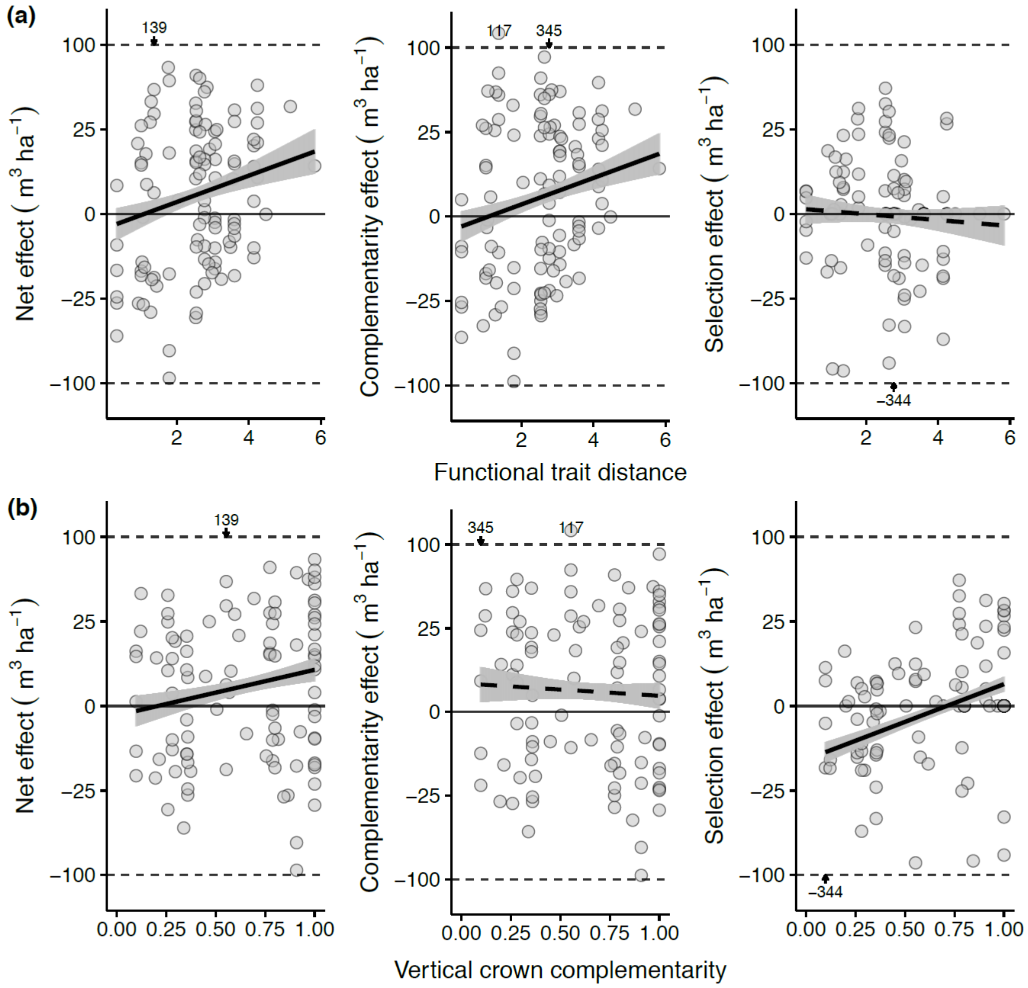


Figure 3 | Relationships between biodiversity effects and (a) functional trait distance and (b) vertical crown complementarity (proportional dissimilarity of monoculture vertical crown extent) in 2016 (n = 108). Regression lines and confidence bands (indicating ± standard error of predicted values) are based on mixed models (Extended Data Table 7). The y-axes are square-root scaled to reflect the quadratic nature of biodiversity effects. Four extreme y-values are moved to the plot margin and given as numbers.

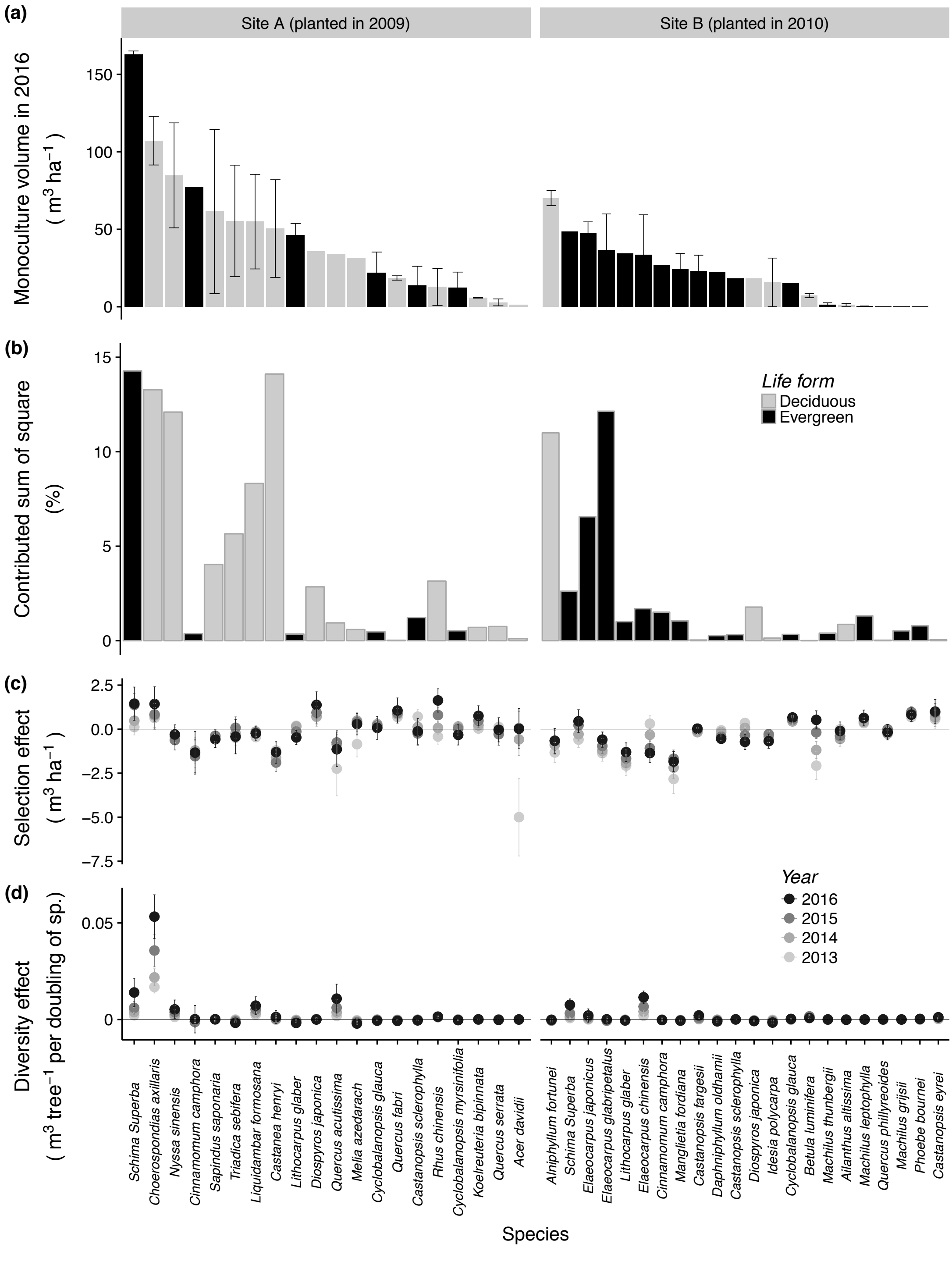


Figure 4 | Monoculture stand-level tree volume of species in 2016 (a) and the fraction of stand-level tree volume sum of squares explained by the presence of each species in a plot (b), their species-specific selection effects (SEs) on stand-level tree volume (c) and their tree-level volume response to species richness (d). Bars indicate standard errors. For (d) the volume of each species, standardized for the number of originally planted individuals of that particular species, was linearly regressed against $\log_2$(tree species richness) with the data from (sub)plots without shrub species.

Table 1 | Mixed-effects models for effects of site, tree species richness (logSR), time (year) and interactions on stand-level tree basal area, stand-level tree volume and their increments.

	Basal area (n = 387)				Volume (n = 387)			
Source of variation	df	ddf	*F*	*P*	df	ddf	*F*	*P*
Site	1	120.0	13.80	<0.001	1	100.8	19.21	<0.001
LogSR	1	111.2	6.00	0.016	1	88.7	5.26	0.024
Year	1	125.5	359.90	<0.001	1	103.0	206.30	<0.001
Site × year	1	125.3	5.80	0.018	1	103.7	18.80	<0.001
LogSR × year	1	117.8	16.00	<0.001	1	94.8	10.83	0.001
	Basal area increment (n = 387)				Volume increment (n = 387)			
Source of variation	df	ddf	*F*	*P*	df	ddf	*F*	*P*
Site	1	123.5	5.10	0.025	1	104.0	14.54	<0.001
LogSR	1	115.7	13.30	<0.001	1	93.9	9.34	0.003
Year	1	111.4	20.90	<0.001	1	104.2	68.85	<0.001
Site × year	1	115.2	4.40	0.037	1	109.2	27.50	<0.001
LogSR × year	1	102.1	10.20	0.002	1	95.1	12.01	<0.001

Notes:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot). Abbreviations: n = numbers of plots in analysis; df = nominator degree of freedom; ddf = denominator degree of freedom; logSR = $\log_2$(tree species richness). *F* and *P* indicate F-ratios and the P-values of the significance test.

EXTENDED DATA

Conversion factors for volume, biomass and carbon content

We harvested 154 trees in a natural forest in 2010 near the experimental sites to determine conversion factors from cylindrical volume (tree basal area × height) to true volume and biomass. The trees belonged to eight common species and three life forms (evergreen, deciduous and coniferous) and were chosen to represent a naturally occurring size span of young trees.

Trees were separated into large woody parts (stems and large branches with a diameter ≥ 3 cm), twigs (the apical part of the stem and large branches plus side branches with a diameter < 3 cm), and dead attached material (large dead branches or twigs). Branches were divided into segments of typically about 1 m length. The volume of large woody parts and twigs was determined geometrically, approximating the parts as truncated cone (large woody parts, $V = \frac{1}{3}\pi(r_1^2+r_1r_2+r_2^2)\times l$ where l is the length and r_1 and r_2 are the end radius), or cone (twigs, as above but r_2=0). The density of these fractions was determined by oven-drying a representative subsample of stem and branch discs or twigs.

These geometric and density data were then scaled up to total aboveground tree biomass using a Bayesian framework, modeling twig mass and density in dependence of branch positions within tree crowns[37].

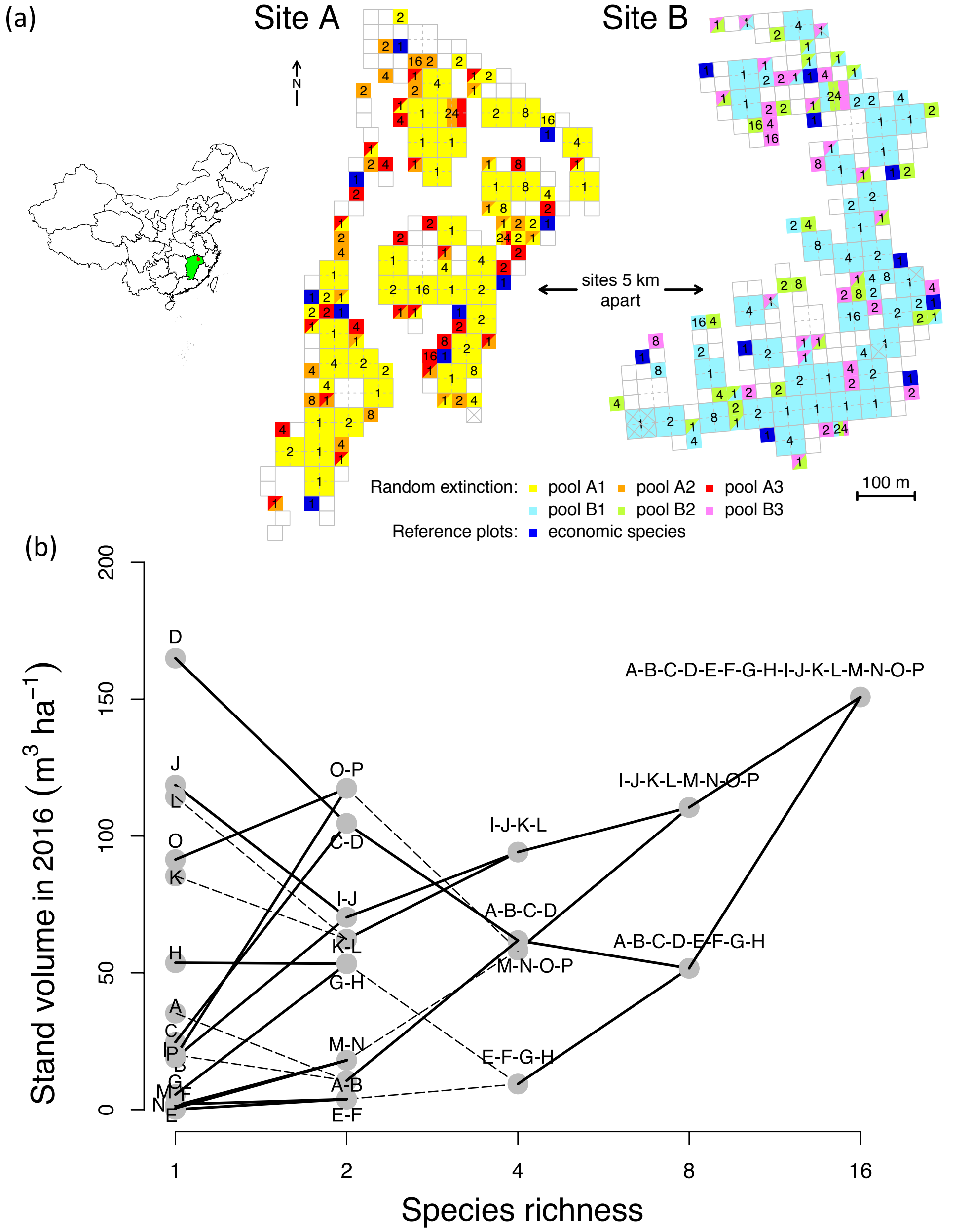
Conversion factors from cylindrical volume to true volume (and mass) were determined as total tree volume (and tree mass, including leaves) divided by cylindrical volume. We analyzed the variation of these conversion factors with tree size and species life form using mixed effects models with species identity as random term. We found that large trees deviated from the linear relationship of form factor and cylindrical volume, and we therefore removed trees with a cylindrical volume ≥ 500 liter from the form factor calibration, leaving a set of 119 trees. Within this set, there was only a small variance among species and no significant effect of life form on the form factor; the form factor decreased linearly with the cylindrical volume of harvested trees (Extended Data Table 3). We therefore used a form factor of 0.5412 m^3 m^{-3}−0.1985 m^{-3} ·BA·h (with basal area BA in m^2 and height h in m). The intercept of 0.5412 m^3 m^{-3} is the weighted average form factor of evergreen and deciduous species at size zero (in our study, 19 of 40 species were evergreen and 21 deciduous). Biomass factors were determined similarly, yielding a conversion factor of 269.13 kg m^{-3}−141.96 kg m^{-3}·BA·h. For the two coniferous species that were planted for comparison in monocultures only, we used separate equations obtained from the harvested trees of the same species *Pinus massoniana* and *Cunninghamia lanceolata*. Here the form factor was 0.5083 m^3 m^{-3}−0.1985 m^{-3} ·BA·h and the biomass factor was 216.79 kg m^{-3}−141.96 kg m^{-3}·BA·h.

Functional trait and phylogenetic distances

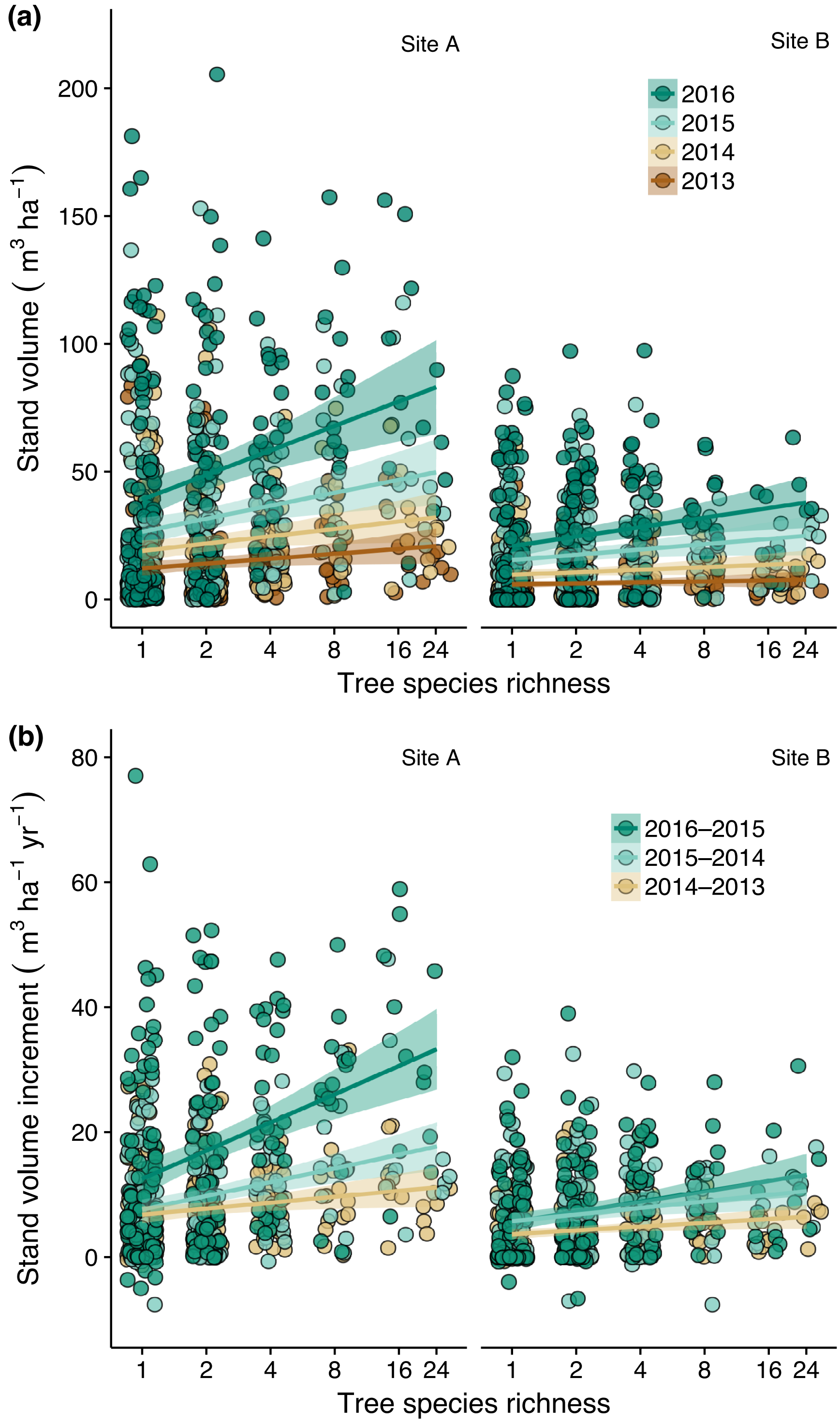
We used four functional traits related to the resource-use strategies of tree species: specific leaf area[38], branch-wood density[38], relative volume growth rate (RGR) and life form (deciduous or evergreen). These traits were determined in plots that were part of the experiment. RGR was calculated as the log-transformed relative difference in stand volume of monocultures between seven (2015 for site A and 2016 for site B) and five years (2013 for site A and 2014 for site B) after planting. We selected the monocultures without shrub treatments. We used site-specific RGR because of the large variation in growth rates between sites A and B. We calculated functional trait distances among species pairs in 2-species communities as Euclidean distances in standardized multivariate trait space (using the four traits as axes).

We calculated phylogenetic distances among species pairs as their cophenetic distance in a node age-calibrated phylogenetic tree[39].

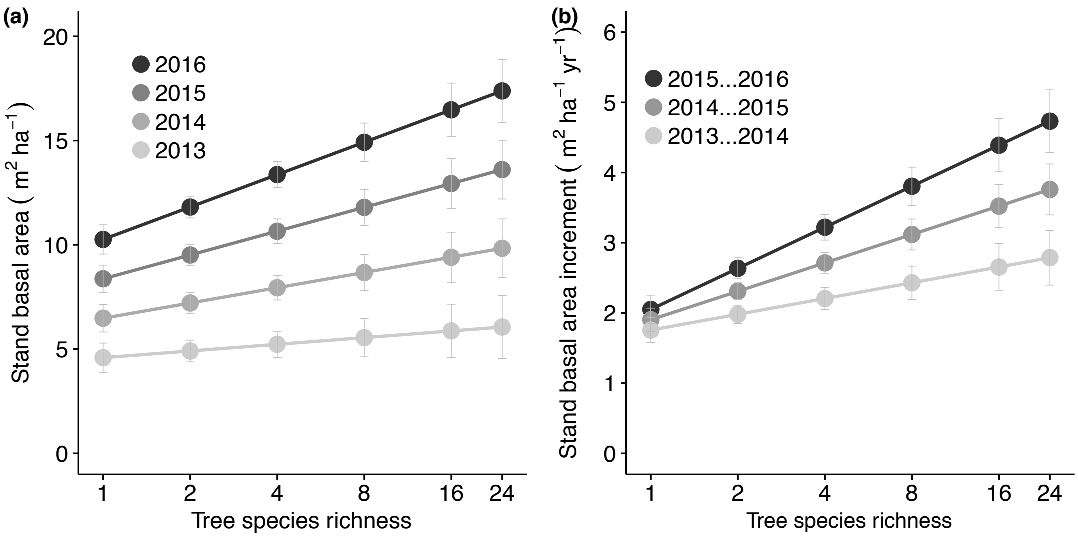
We assessed the effects of trait and phylogenetic distances on different components of diversity effects of two-species mixtures with linear mixed-effects models, where we set site and trait/phylogenetic distance as fixed effects, community composition and plot as random effect (with a separate variance component for each site). Measures of diversity effects were square-root transformed with sign reconstruction to improve normality of model residuals.



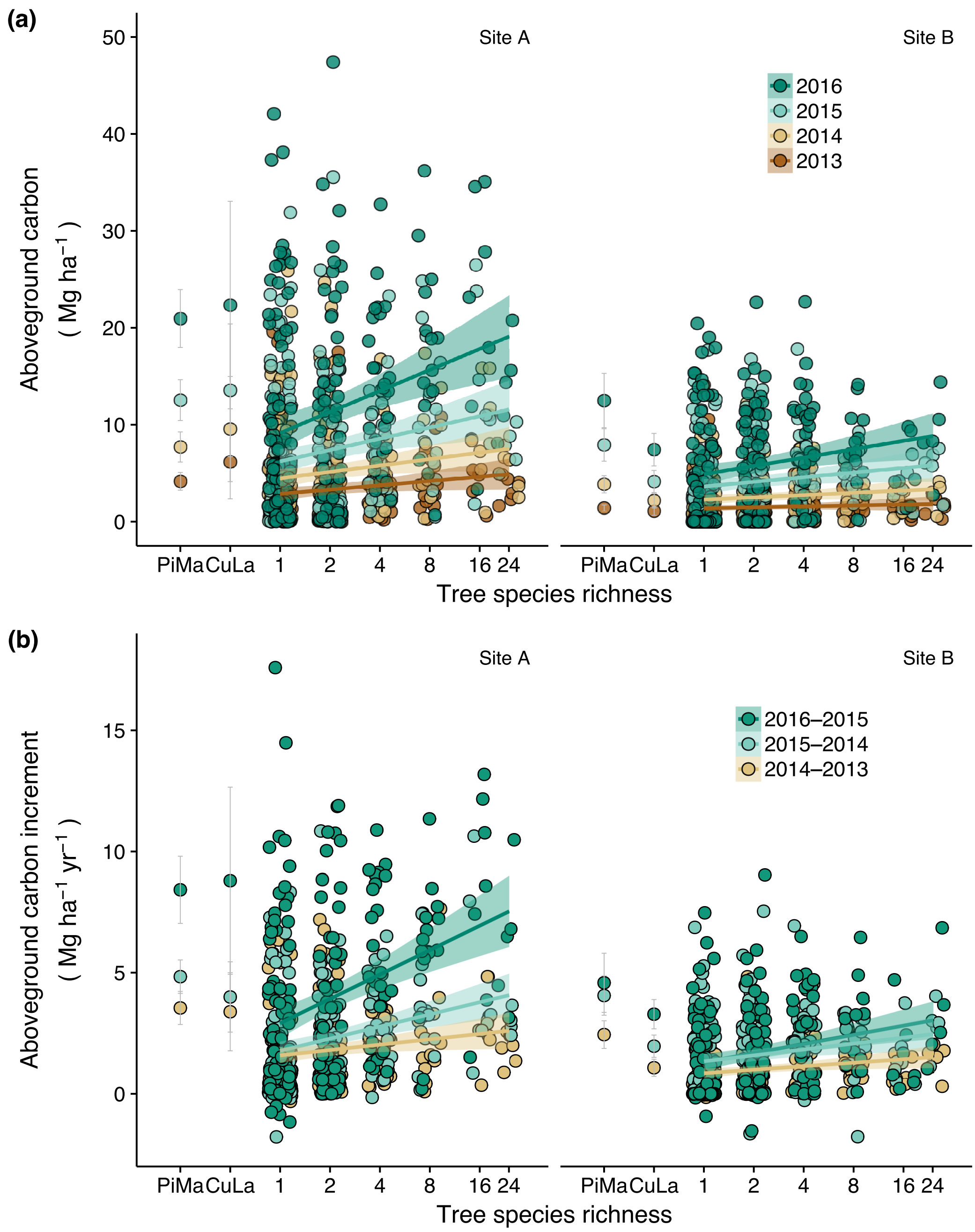
Extended Data Figure 1 | Map of BEF-China position and experimental plots of random extinction scenarios and economic trees (a). Results from species pool A1 to illustrate the "broken stick" design (b). Letters represent different species (A= *Cyclobalanopsis glauca;* B = *Quercus fabri;* C = *Rhus chinensis*; D = *Schima superba*; E = *Castanopsis eyrei*; F = *Cyclobalanopsis myrsinifolia*; G = *Koelreuteria bipinnata*; H = *Lithocarpus glaber*; I = *Castanea henryi*; J = *Nyssa sinensis*; K = *Liquidambar formosana*; L = *Sapindus saponaria*; M = *Castanopsis sclerophylla*; N = *Quercus serrata*; O = *Choerospondias axillaris*; P = *Triadica sebifera*). Solid lines represent overyielding, while dashed lines represent underyielding.



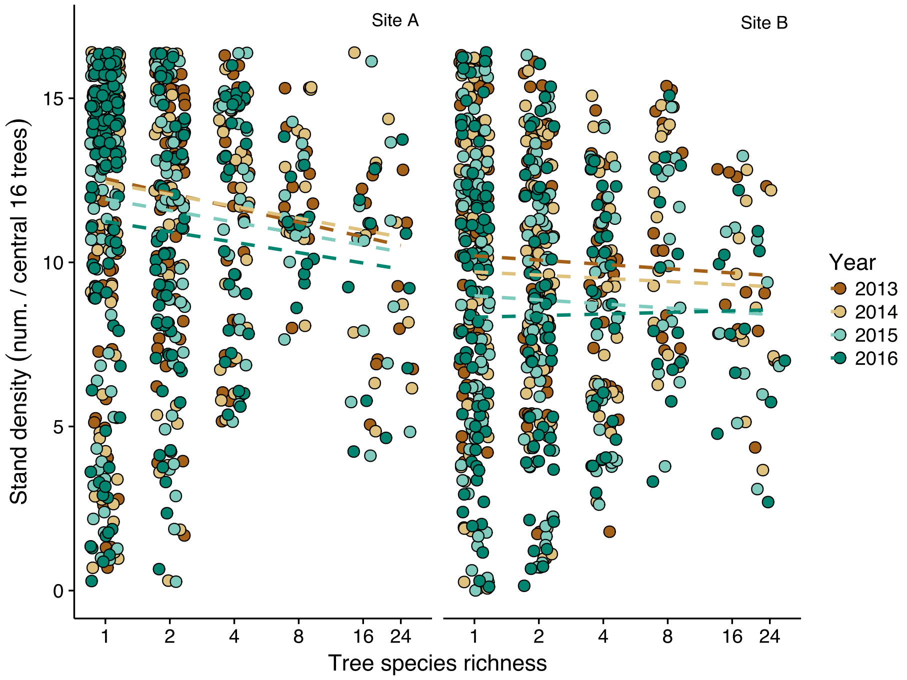
Extended Data Figure 2 | Stand-level tree volume (a) and its increment (b) as a function of tree species richness from 2013–2016. Positive effects of tree species richness increase with time. Raw data points, regression lines and 95% confidence bands are shown for each year. Note that the extremes of the point cloud necessarily taper off towards higher diversity levels for statistical rather than biological reasons; this is due to the fact that for a given diversity level extreme values are more extreme the larger the sample size is[26].



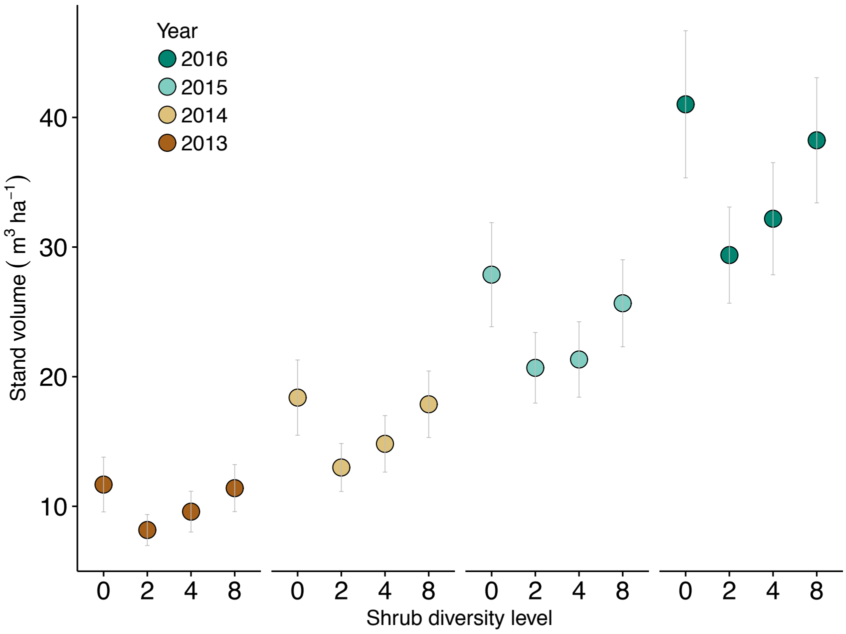
Extended Data Figure 3 | Stand-level tree basal area (a) and its annual increment (b) as a function of tree species richness from 2013–2016. The figure shows predicted means and standard errors based on fitted mixed models (Table 1). Effects of species richness were significantly positive and increased throughout the observation period.



Extended Data Figure 4 | Aboveground stand-level tree carbon (a) and its annual increment (b) as a function of tree species richness from 2013–2016. Raw data points, regression lines and 95% confidence bands are shown. On the left of each panel means ± standard errors for the two economic tree species (PiMa = *Pinus massoniana*; CuLa = *Cunninghamia lanceolata*) are inserted. Note that the extremes of the point cloud necessarily taper off towards higher diversity levels for statistical reasons; this is due to the fact that for a given diversity level extreme values are more extreme the larger the sample size is[26].



Extended Data Figure 5 | Stand density as a function of tree species richness from 2013–2016. Raw data points together with non-significant regression lines (dashed) are shown. Density indicates the number of surviving trees out of 16 planted in the central area of each plot.



Extended Data Figure 6 | Effects of shrub diversity on average stand-level tree volume in species pools A1 and B1. Data are from 4mu plots. The figure shows predicted means and standard errors based on a fitted mixed model (Extended Data Table 8).

Extended Data Table 1 | List of tree species used in the BEF-China experiment according to the Flora of China (http://www.efloras.org and http://frps.eflora.cn).

Species	Abbre-viation	Site	Type
Acer davidii Franchet	AcDa	A	Deciduous
Ailanthus altissima (Miller) Swingle	AiAl	B	Deciduous
Alniphyllum fortunei (Hemsley) Makino	AlFo	B	Deciduous
Betula luminifera H. Winkler in Engler	BeLu	B	Deciduous
Castanea henryi (Skan) Rehd. et Wils.	CaHe	A	Deciduous
Castanopsis carlesii (Hemsley) Hayata	CaCa	A	Evergreen
Castanopsis eyrei (Champion ex Bentham) Tutcher	CaEy	AB	Evergreen
Castanopsis fargesii Franchet	CaFa	B	Evergreen
Castanopsis sclerophylla (Lindley & Paxton) Schottky	CaSc	AB	Evergreen
Celtis biondii Pampanini	CeBi	B	Deciduous
Choerospondias axillaris (Roxb.) Burtt et Hill	ChAx	A	Deciduous
Cinnamomum camphora (Linnaeus) J. Presl in Berchtold & J. Presl	CiCa	AB	Evergreen
Cunninghamia lanceolata (Lamb.) Hook.	CuLa	AB	Evergreen
Cyclobalanopsis glauca (Thunberg) Oersted	CyGl	AB	Evergreen
Cyclobalanopsis myrsinifolia (Blume) Oersted	CyMy	A	Evergreen
Daphniphyllum oldhamii (Hemsley) K. Rosenthal in Engler	DaOl	AB	Evergreen
Diospyros japonica Siebold & Zuccarini; (Old name: *Diospyros glaucifolia*)	DiGl	AB	Deciduous
Elaeocarpus chinensis (Gardner & Champion) J. D. Hooker ex Bentham	ElCh	B	Evergreen
Elaeocarpus glabripetalus Merrill	ElGl	B	Evergreen
Elaeocarpus japonicus Siebold & Zuccarini	ElJa	B	Evergreen
Idesia polycarpa Maximowicz	IdPo	B	Deciduous
Koelreuteria bipinnata Franch.	KoBi	A	Deciduous
Liquidambar formosana Hance	LiFo	A	Deciduous
Lithocarpus glaber (Thunb.) Nakai	LiGl	AB	Evergreen
Machilus grijsii Hance	MaGr	B	Evergreen
Machilus leptophylla Handel-Mazzetti	MaLe	B	Evergreen
Machilus thunbergii Siebold & Zuccarini	MaTh	B	Evergreen

Manglietia fordiana Oliver; (Old name: *Manglietia yuyuanensis*)	MaYu	B	Evergreen
Melia azedarach Linnaeus	MeAz	A	Deciduous
Meliosma flexuosa Pampanini	MeFl	B	Deciduous
Nyssa sinensis Oliver	NySi	A	Deciduous
Phoebe bournei (Hemsley) Yen C. Yang	PhBo	B	Evergreen
Pinus massoniana Lamb.	PiMa	AB	Deciduous
Quercus acutissima Carruthers	QuAc	A	Deciduous
Quercus fabri Hance	QuFa	A	Deciduous
Quercus phillyreoides A. Gray	QuPh	B	Evergreen
Quercus serrata Murray	QuSe	A	Deciduous
Rhus chinensis Mill.	RhCh	A	Deciduous
Sapindus saponaria Linnaeus; (Old name: *Sapindus mukorossi*)	SaMu	A	Deciduous
Schima superba Gardn. et Champ.	ScSu	AB	Evergreen
Triadica cochinchinensis Loureiro; (Old name: *Sapium discolor*)	SaDi	A	Deciduous
Triadica sebifera (L.) Small; (Old name: *Sapium sebiferum*)	SaSe	A	Deciduous

Notes:

The site column shows the experimental site (A, B) where the species was planted. The type column shows species life form (D = deciduous species; E = evergreen species).

Extended Data Table 2 | Experimental design

Site	Pool	Species richness	Plot size	Shrubs	Species composition															
A	A1	16	4mu/1mu	yes	CyGl	QuFa	RhCh	ScSu	CaEy	CyMy	KoBi	LiGl	CaHe	NySi	LiFo	SaMu	CaSc	QuSe	ChAx	SaSe
		8	4mu/1mu	yes	CyGl	QuFa	RhCh	ScSu	CaEy	CyMy	KoBi	LiGl	CaHe	NySi	LiFo	SaMu	CaSc	QuSe	ChAx	SaSe
		4	4mu/1mu	yes	CyGl	QuFa	RhCh	ScSu	CaEy	CyMy	KoBi	LiGl	CaHe	NySi	LiFo	SaMu	CaSc	QuSe	ChAx	SaSe
		2	4mu/1mu	yes	CyGl	QuFa	RhCh	ScSu	CaEy	CyMy	KoBi	LiGl	CaHe	NySi	LiFo	SaMu	CaSc	QuSe	ChAx	SaSe
		1	4mu/1mu	yes	CyGl	QuFa	RhCh	ScSu	CaEy	CyMy	KoBi	LiGl	CaHe	NySi	LiFo	SaMu	CaSc	QuSe	ChAx	SaSe
	A2	16	1mu	no	CaCa	LiGl	AcDa	MeAz	CaEy	KoBi	CiCa	CyMy	DiGl	NySi	SaDi	ScSu	DaOl	QuFa	QuAc	SaMu
		8	1mu	no	CaCa	LiGl	AcDa	MeAz	CaEy	KoBi	CiCa	CyMy	DiGl	NySi	SaDi	ScSu	DaOl	QuFa	QuAc	SaMu
		4	1mu	no	CaCa	LiGl	AcDa	MeAz	CaEy	KoBi	CiCa	CyMy	DiGl	NySi	SaDi	ScSu	DaOl	QuFa	QuAc	SaMu
		2	1mu	no	CaCa	LiGl	AcDa	MeAz	CaEy	KoBi	CiCa	CyMy	DiGl	NySi	SaDi	ScSu	DaOl	QuFa	QuAc	SaMu
		1	1mu	no	CaCa	LiGl	AcDa	MeAz	CaEy	KoBi	CiCa	CyMy	DiGl	NySi	SaDi	ScSu	DaOl	QuFa	QuAc	SaMu
	A3	16	1mu	no	AcDa	QuAc	CaHe	RhCh	CaSc	CiCa	LiFo	MeAz	CaCa	CyGl	SaDi	SaSe	ChAx	DiGl	DaOl	QuSe
		8	1mu	no	AcDa	QuAc	CaHe	RhCh	CaSc	CiCa	LiFo	MeAz	CaCa	CyGl	SaDi	SaSe	ChAx	DiGl	DaOl	QuSe
		4	1mu	no	AcDa	QuAc	CaHe	RhCh	CaSc	CiCa	LiFo	MeAz	CaCa	CyGl	SaDi	SaSe	ChAx	DiGl	DaOl	QuSe
		2	1mu	no	AcDa	QuAc	CaHe	RhCh	CaSc	CiCa	LiFo	MeAz	CaCa	CyGl	SaDi	SaSe	ChAx	DiGl	DaOl	QuSe
		1	1mu	no	AcDa	QuAc	CaHe	RhCh	CaSc	CiCa	LiFo	MeAz	CaCa	CyGl	SaDi	SaSe	ChAx	DiGl	DaOl	QuSe
B	B1	16	4mu/1mu	yes	AiAl	MeFl	IdPo	MaGr	CeBi	ElGl	ElJa	PhBo	BeLu	CaFa	MaYu	QuPh	ElCh	MaTh	AlFo	MaLe
		8	4mu/1mu	yes	AiAl	MeFl	IdPo	MaGr	CeBi	ElGl	ElJa	PhBo	BeLu	CaFa	MaYu	QuPh	ElCh	MaTh	AlFo	MaLe
		4	4mu/1mu	yes	AiAl	MeFl	IdPo	MaGr	CeBi	ElGl	ElJa	PhBo	BeLu	CaFa	MaYu	QuPh	ElCh	MaTh	AlFo	MaLe
		2	4mu/1mu	yes	AiAl	MeFl	IdPo	MaGr	CeBi	ElGl	ElJa	PhBo	BeLu	CaFa	MaYu	QuPh	ElCh	MaTh	AlFo	MaLe
		1	4mu/1mu	yes	AiAl	MeFl	IdPo	MaGr	CeBi	ElGl	ElJa	PhBo	BeLu	CaFa	MaYu	QuPh	ElCh	MaTh	AlFo	MaLe
	B2	16	1mu	no	CaEy	CeBi	MaLe	PhBo	DiGl	LiGl	ElGl	MaTh	AiAl	AlFo	CaFa	CaSc	CyGl	ScSu	CiCa	DaOl
		8	1mu	no	CaEy	CeBi	MaLe	PhBo	DiGl	LiGl	ElGl	MaTh	AiAl	AlFo	CaFa	CaSc	CyGl	ScSu	CiCa	DaOl
		4	1mu	no	CaEy	CeBi	MaLe	PhBo	DiGl	LiGl	ElGl	MaTh	AiAl	AlFo	CaFa	CaSc	CyGl	ScSu	CiCa	DaOl
		2	1mu	no	CaEy	CeBi	MaLe	PhBo	DiGl	LiGl	ElGl	MaTh	AiAl	AlFo	CaFa	CaSc	CyGl	ScSu	CiCa	DaOl
		1	1mu	no	CaEy	CeBi	MaLe	PhBo	DiGl	LiGl	ElGl	MaTh	AiAl	AlFo	CaFa	CaSc	CyGl	ScSu	CiCa	DaOl
	B3	16	1mu	no	BeLu	DaOl	CaEy	QuPh	CyGl	MaGr	ElJa	LiGl	CaSc	IdPo	ElCh	MaYu	CiCa	DiGl	MeFl	ScSu
		8	1mu	no	BeLu	DaOl	CaEy	QuPh	CyGl	MaGr	ElJa	LiGl	CaSc	IdPo	ElCh	MaYu	CiCa	DiGl	MeFl	ScSu
		4	1mu	no	BeLu	DaOl	CaEy	QuPh	CyGl	MaGr	ElJa	LiGl	CaSc	IdPo	ElCh	MaYu	CiCa	DiGl	MeFl	ScSu
		2	1mu	no	BeLu	DaOl	CaEy	QuPh	CyGl	MaGr	ElJa	LiGl	CaSc	IdPo	ElCh	MaYu	CiCa	DiGl	MeFl	ScSu
		1	1mu	no	BeLu	DaOl	CaEy	QuPh	CyGl	MaGr	ElJa	LiGl	CaSc	IdPo	ElCh	MaYu	CiCa	DiGl	MeFl	ScSu

Note:

See Extended Data Table 1 for species abbreviations.

Extended Data Table 3 | Mixed-effects model for the effects of cylindrical volume and life form on form and biomass factors.

	Form factor				Biomass factor			
	Df	ddf	*F*	*P*	ddf	denDF	*F*	*P*
(Intercept)	1	4.4	2418	<0.001	1	4.8	828.9	<0.001
Cylindrical volume	1	105.7	8	0.007	1	114.7	11.2	0.001
Life form	2	4.7	20	0.005	2	4.9	22.1	0.004
Variance components		Component	s.e.	z-ratio		Component	s.e.	z-ratio
Species identity		0.00002	0.00058	0.043		257.90	356.87	0.723
Residual		0.01237	0.00169	7.321		4384.52	590.66	7.423

Notes:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (the random term was species identity). Abbreviations: df = nominator degree of freedom; ddf = denominator degree of freedom; s.e. = standard error; *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 4 | Mixed-effects models for the effects of site, tree species richness (logSR), time (year) and interactions on aboveground stand-level tree carbon and its increment.

Source of variation	Aboveground carbon				Aboveground carbon increment			
	df	ddf	*F*	*P*	df	ddf	*F*	*P*
Site	1	101.30	19.12	<0.001	1	104.70	14.42	<0.001
LogSR	1	89.20	5.16	0.026	1	94.60	9.11	0.003
Year	1	104.20	209.50	<0.001	1	106.20	70.30	<0.001
Site × year	1	104.80	18.47	<0.001	1	110.60	26.78	<0.001
LogSR × year	1	95.90	10.54	0.002	1	97.00	11.63	<0.001

Notes:

Fixed effects were fitted sequentially (type I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot). Abbreviations: df = nominator degree of freedom; ddf = denominator degree of freedom; logSR = $\log_2$(tree species richness). *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 5a | Average number of 1-mu (sub)plots with overyielding (Over) and underyielding (Under) for stand-level tree volume in 2016 across richness levels.

		All plots			Transgressive plots		
Reference	Target -> reference	Over	Under	*P* (over>under)	Over	Under	*P* (over>under)
Component monocultures	2->1	65	47	0.088	43	21	0.005
	4->1	39	17	0.003	14	0	<0.001
	8->1	21	7	0.007	3	0	0.041
	16->1	9	5	0.280	1	0	0.239
	total	134	76	<0.001	62	21	<0.001
Component mixtures with half the number of species	2->1	65	47	0.088	43	22	0.009
	4->2	32	24	0.284	20	9	0.039
	8->4	17	11	0.250	10	6	0.315
	16->8	7	7	1.000	6	5	0.763
	total	121	89	0.027	79	42	<0.001

Extended Data Table 5b | Average number of 1-mu (sub)plots with overyielding (Over) and underyielding (Under) for stand-level tree volume in different years.

Refeerence	Year	All plots			Transgressive plots		
		Over	Under	*P* (over>under)	Over	Under	*P* (over>under)
Component monocultures	2013	126	84	0.004	50	20	<0.001
	2014	128	82	0.001	61	21	<0.001
	2015	133	77	<0.001	60	24	<0.001
	2016	134	76	<0.001	61	21	<0.001
Component mixtures with half the number of species	2013	112	98	0.33	69	37	0.002
	2014	111	99	0.41	74	40	0.001
	2015	115	95	0.17	73	43	0.005
	2016	121	89	0.027	79	42	<0.001

Notes:

P-values indicate significance of differences between the numbers of overyielding vs. underyielding plots (χ^2-test), or between transgressively overyielding vs. transgressively underyielding plots.

Extended Data Table 6 | Mixed-effects models for the effects of site, tree species richness (logSR), time (year) and the interaction of the latter two on the biodiversity effects NE, CE and SE.

	NE				CE				SE			
	df	ddf	*F*	*P*	df	ddf	*F*	*P*	df	ddf	*F*	*P*
Intercept	1	60.7	20.43	<0.001	1	50.7	43.54	<0.001	1	52.7	9.29	0.004
Site	1	64.5	0.18	0.675	1	58.9	2.69	0.107	1	59.7	3.74	0.058
LogSR	1	60.5	4.58	0.036	1	50.6	9.79	0.003	1	52.6	5.89	0.019
Year	1	47.7	23.61	<0.001	1	31.3	9.61	0.004	1	37.3	4.61	0.038
LogSR × year	1	47.1	0.81	0.374	1	31.1	0.26	0.617	1	37.0	0.24	0.627

Notes:

Biodiversity effects were square-root transformed with sign reconstruction ($\mathrm{sign}(y)\sqrt{|y|}$). Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot). Abbreviations: df = nominator degree of freedom; ddf = denominator degree of freedom. *F* and *P* indicate F-ratios and P-values of the significance tests. The first line "Intercept" shows that the overall mean for all biodiversity effects differs significantly from zero (positively for NE and CE, negatively for SE).

Extended Data Table 7 | Mixed-effects models for the effects of functional distance (FD), phylogenetic distance (PD) or vertical crown complementarity (PDS) on the biodiversity effects NE, CE and SE in 2-species tree stands.

	NE				CE				SE			
	df	ddf	*F*	*P*	df	ddf	*F*	*P*	df	ddf	*F*	*P*
FD	1	34.6	4.34	0.045	1	17.3	5.09	0.037	1	94	0.28	0.600
PD	1	58.4	0.92	0.342	1	76.3	0.07	0.787	1	39.4	0.67	0.420
PDS	1	22.5	3.43	0.077	1	56.5	0.20	0.659	1	8.2	26.43	< 0.001

Notes:

Biodiversity effects were square-root transformed with sign reconstruction ($\text{sign}(y)\sqrt{|y|}$). The effects of FD, PD and PDS were fitted after site (random terms were species composition and plot, considering a separate variance component for each site). Abbreviations: df = nominator degree of freedom; ddf = denominator degree of freedom. *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 8 | Mixed-effects model for the effects of site, tree species richness (logSR), shrub presence, plot size, shrub species richness (logShrubSR), time (year) and interactions on stand-level tree volume. Data are from species pool A1 and B1, which include a shrub treatment in the planting design.

Source of variation	df	ddf	*F*	*P*
Site	1	46.2	12.20	0.001
LogSR	1	45.0	3.70	0.059
Shrub presence	1	233.5	4.80	0.029
Plot size	1	116.2	0.90	0.353
LogShrubSR	1	198.8	5.40	0.022
Year	1	46.9	86.80	<0.001
LogSR × shrub presence	1	232.2	0.80	0.380
LogSR × plot size	1	114.2	0.20	0.694
LogSR × logShrubSR	1	198.8	0.30	0.606
LogSR × year	1	46.9	7.20	0.010
Shrub presence × year	1	235.1	9.50	0.002
Plot size × year	1	128.7	0.00	0.942
LogShrubSR × year	1	197.1	3.30	0.069

Notes:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot). Abbreviations: df = nominator degree of freedom; ddf = denominator degree of freedom; logSR = $\log_2$(tree species richness); logShrubSR = $\log_2$(shrub species richness — this term is aliased with shrub presence and plot size and therefore fitted after these to only test for effects of shrub species richness in sub-plots of large plots where shrubs were present). *F* and *P* indicate F-ratios and P-values of the significance tests.

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Chapter 2

Do negative density-dependent effects of consumers and pathogens drive plant diversity–productivity relationships in a subtropical forest? An experimental test in a large-scale afforestation.

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Do negative density-dependent effects of consumers and pathogens drive plant diversity–productivity relationships in a subtropical forest? An experimental test in a large-scale afforestation.

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ABSTRACT

Complementarity effects are discussed as drivers of diversity–ecosystem functioning (BEF) relationships in forest ecosystems, but the importance of the resistance to leaf pathogens and herbivores in higher diversity forest as one of the mechanisms for the BEF relationship is unknown. Here we conducted an experiment in a newly established large forest biodiversity–ecosystem functioning experiment in JiangXi Province, China (BEF-China). Using experimental manipulations of pathogens, herbivores across 6 biodiversity levels (1, 2, 4, 8, 16, 24 species), we assessed the relative importance of herbivore and pathogen release as mechanisms driving diversity–productivity relationships in a subtropical forest. We found that the pathogen exclusion treatment significantly weakened the positive relationship between species richness and tree productivity, while the effects from herbivore exclusion treatment were same for both low and high diversity levels. These results support the hypothesis that greater leaf pathogen pressure inhibits productivity in low diversity plots while there was weak support for a functional role of insect herbivore. Our results contribute to the mechanistic understanding of this relationship in subtropical forest, which can help to conserve tropical biodiversity and improve productivity, thus help mitigating climate change.

Keywords: BEF-China, leaf pathogens and herbivores, negative density dependence, biodiversity, primary production, niche complementarity

INTRODUCTION

Positive effects of species richness on primary productivity have been found in many experimental studies (Tilman *et al.* 2001; Morin *et al.* 2011; Hooper *et al.* 2012), but the biological mechanisms that drive these responses remain largely elusive, despite decades of research. Also, most research to date has addressed biodiversity–ecosystem functioning (BEF) relationships in herbaceous ecosystems, with comparably little that is known about biodiversity effects in forest, in particular outside the temperate zone.

Biodiversity effects ultimately depend on interspecific niche differences. The use of complementary resources can reduce competition among species, thereby promoting the productivity of species-rich communities (Tilman *et al.* 1997). However, how exactly and which resources species partition is difficult to determine (von Felten *et al.* 2009). Statistical approaches have widely been used to tentatively attribute biodiversity effects to particular groups of mechanisms. One of the most important such method is the additive partitioning scheme which allows to decompose the overyielding of mixed communities into complementarity and selection effects (Loreau & Hector 2001). Complementarity effects typically arise when the benefit of growing in species mixtures is distributed among many species. In contrast, selection effects indicate that the community-level performance is dominated by contributions of one or few species with suitable traits, whereas other subordinate species suffer from competition by dominants. While such analyses have proven useful (Fargione *et al.* 2007), they are limited in that they do not help to identify the specific biological mechanisms through which species interact.

Conspecific negative density dependence is a widespread population-level phenomenon that is thought to contribute to the coexistence of species, in particular in highly diverse communities. It occurs because population growth is curtailed by crowding, by trophic interactions including consumers and pathogens, and by direct competition (Petermann *et al.* 2008). An important example is seed predation, which often was found to be higher in areas in which the respective species reach a high density (Clark & Clark 1984; Bagchi *et al.* 2014). Many insect herbivores and fungal pathogens show some degree of host specificity, and they thus mediate similar density-dependent effects, which may modulate tree growth and thereby structure forest communities (Terborgh 2012; Dostal *et al.* 2013; Bagchi *et al.* 2014). Conversely, several recent studies with herbaceous species suggest that not only complementary resource use but also interspecific differentiation of pathogen and consumer-related niches promote BEF-relationships (Petermann *et al.* 2008; Maron *et al.* 2011; Schnitzer *et al.* 2011; Zuppinger-Dingley *et al.* 2016).

Low latitude forests exhibit a species diversity that by far exceeds the one of temperate and boreal forests, suggesting that different mechanisms structure communities in different biomes. Interestingly, neutral models are remarkably successful in predicting fundamental ecological patterns such as species-area relationships and species abundance distributions in highly diverse forests (Bell 2001, Hubbell 2001). It therefore has been speculated that niche-based complementarity may be less important in these communities (Hubbell 2006). If this indeed were the case, this would result in weaker BEF relationships.

Subtropical and tropical forests generally show higher herbivory rates and pathogen loads than temperate forest (Novotny *et al.* 2006). These trophic interactions thus likely are more important modulators of community-level productivity in low latitude forest than in temperate forest. Also, niche differentiation among species with respect to pathogen and consumer interactions may be relatively more important in species rich low-latitude forest, which would promote enemy-mediated BEF effects if these were density-dependent. However, a higher diversity of trees may also lead to a shift from specialist to generalist herbivores and pathogens, or promote populations of these enemies through dietary mixing and habitat improvement through environmental heterogeneity (Schuldt *et al.* 2010), which would counteract the negative density-dependent enemy effects that promote positive BEF relationships.

In summary, BEF relationships have predominantly been investigated in herbaceous plant communities, with few BEF experiments in forest and most of these located in the temperate zone. The underrepresentation of highly diverse forest ecosystems in BEF research appears critical in the light of species interactions that differ in importance among biomes. Trophic interactions probably are relatively more important in species rich forest, and therefore are more likely to support BEF relationships through negative density-dependent effects, but this has not been tested experimentally to date.

To address this question, we combined factorial insecticide and fungicide treatments with a tree species richness treatment in a large scale forest biodiversity experiment in subtropical China (Bruelheide *et al.* 2014). The experimental plots contained 1 to 16 tree species that had been growing for 6–7 years when the pesticide treatments were applied to subplots for an additional two years. We monitored tree growth in pesticide-treated and control plots, together with measurement of leaf fungal infestation and herbivore damage. Specifically, we predicted that the suppression of enemy-mediated impacts by pesticides would dampen BEF relationships because these were mediated by negative density-dependent effects of enemies. We further hypothesized that fast-growing trees would benefit more strongly from enemy release because these were more susceptible to infestation and because they made up for a higher share of foliage in the community and produced leaves that were of higher quality to these enemies.

METHODS

Study site and experimental design

In 2009–2010, a large-scale forest biodiversity experiment was established at two sites (A and B) that each span approximately 20 ha. A total of 566 plots were planted with 400 trees arranged on a 20 × 20 grid with 1.29 m distance between neighbors. Using two independent pools of 24 species per site, we simulated a random, trait-independent reduction of tree species richness from 24 to 1. This was achieved by first randomly dividing the full set of 24 species into three pools of 16 species that overlapped by 8 species each. These 16 species pools were then divided into non-overlapping halves, creating six distinct 8-species mixtures per site. This procedure was repeated until monocultures were obtained (Bruelheide *et al.* 2014). This “broken stick” design ensured that all species were equally represented at all diversity levels, i.e. the average fraction of species found across the plots did not vary with species richness. In present study, we only used plots from one species pool in each site, resulting into 62 plots for the both sites. All plots were weeded once a year, with all upcoming vegetation between the planted trees being removed.

In April 2014, we established subplot-level treatments in subplots that contained 16 trees each. These subplots were arranged along one edge of the main plots and contained 4 × 4 trees on an area of 5.16 × 5.16 m^2. Three experimental treatments were randomly assigned to one subplot per plot: fungicide application (F), insecticide application (I), and no treatment (control plot, C). The study included two further treatments (phosphorus fertilizer application [P] and lack of weeding [W]), but these are not part of the present analysis. We used a mixture of 10 mL dimethoate (an organophosphate) and 10 mL deltamethrin (a pyrethroid) that was dissolved in 4 L of water. We used 8 g of mancozeb (a dithiocarbamate) and 25 mL of myclobutanil (a triazole) that were dissolved in a total of 4 L of water. Insecticide and fungicide solutions were then sprayed over tree crowns every 4 weeks (every 2 weeks during the rainy season because of more rapid leaching), but only on days with no or very little wind. The control plots (C) were sprayed with 4 L of water.

Tree inventory

In September of the years 2014, 2015 and 2016, basal diameter and height of all trees in the subplots were measured. We further assessed the size of the central 16 trees in each main plot (the regular inventories were conducted in the plot’s central area). A proxy of tree volume was then calculated by multiplying the basal area of each tree with its height.

Leaf damage assessment

We quantified the leaf damage created by herbivores and fungal pathogens in monocultures of the investigated species. In September 2016, we randomly chose five individuals for each species from the central 6 × 6 trees of the main monoculture plot. We then randomly picked three branches from different canopy layers, and sampled seven young, fully expanded leaves per branch. We then classified all leaves into one of six damage classes (0, <5, <25, <50, <75, and >75% of the leaf's area affected), separately for herbivory and fungal damage. For statistical analyses, we used the classes' central values as independent variable (e.g. 0.025 for the 0–5% class). Data were available for 30 of the 32 species; *Meliosma flexuosa* monocultures were not planted due to a lack of seedlings and *Celtis biondii* individuals died throughout the experiment.

Statistical analysis

All data were analyzed by general linear mixed models summarized by ANOVA. Models were fitted by restricted maximum likelihood using ASReml 3.0 (Butler et al., 2007) in R 3.3 (http://r-project.org). Site, species richness, insecticide and fungicide application, the interaction of insecticide and fungicide application with species richness, year, and the interaction of the experimental treatments with year were fitted as fixed effects. Plot, which in our design is equivalent to community composition, and plot × year were fitted as random effects. The dependent variables were tree basal area or the tree volume proxy. We analyzed all data untransformed because data transformation would introduce spurious diversity effects (see Schmid *et al.* 2017). Heteroscedastic residual variances that occurred because the sites had been planted in different years, and trees therefore differed in size, were accounted for by fitting separate variance components for each site (idh option of ASReml).

Overyielding was defined as the stand level tree volume proxy higher than that would be expected based on constituent monocultures. We partitioned net diversity effect into selection effect and complementarity effect with Loreau and Hector (2001) additive partition method. Thus complementarity effect was calculated by the difference of net effect and selection effect (calculated by the correlation between the relative yield and monoculture productivity). We used the variable of stand basal area increase because of the high variation of stand volume increase.

Pearson product-moment correlation coefficient was computed to access the relationship between the species leaf traits (SLA and C/N) (Kröber *et al.* 2015) and pest load. Simple linear regression was used to test the relationship between the species traits and pesticide effects on the BEF relationship.

Pesticide effects on species population performance in each diversity level were calculated by the differences between the stand volume increase in pesticide plots and control plots. Coefficients of the slope for the relationship between species richness and pesticide effects were computed by simple linear regression. Negative slope means this species benefits more from pest exclusion in lower diversity levels than higher levels.

RESULTS

Community-level

Stand basal area and stand volume, as well as their increase in 2015 and 2016 increased statistically significantly with tree species richness (Fig. 1; Tables 1, 2). The productivity of control subplots and main plots did not differ significantly (Table 1, $F_{1,\,51.4} = 2.01$, $P = 0.16$). Importantly, effects of tree species richness on the observed variables did not differ between main plot and control subplot (Table 1, plot-type × log(species richness): $F_{1,53.5} = 1.22$, $P = 0.3$).

Neither insecticide nor fungicide application altered the productivity of tree communities when averaged across the species richness gradient (Table 2; $P > 0.5$ for both fungicide and insecticide treatment). Fungicide application, however, resulted in an increased stand-level basal area and volume in monoculture but not mixture plots, which evidenced in a statistically significant interaction between log(species richness) and fungicide treatment (Fig. 1; Table 2; $F_{1,111.7} = 6.90$, $P = 0.01$). This interaction was so important that the positive tree species richness effect vanished under fungicide application (Fig 1). Insecticide application did not result in similar effects (Fig 1, Table 2, $F_{1,106.2} = 0.20$, $P = 0.7$).

Population-level

Species within a community differed significantly in their response to fungicide and insecticide application (Fig. 2a, b; Fig. S2, S3). Some species benefit with pesticide in monoculture more than mixture (negative slope), while others performed well rather in mixture after pesticide (positive slope). These differentiations for the fungicide treatments (Fig. 2a, Fig. S2) can be explained by leaf pathogen load in the central of monoculture plots (Fig. 2c, $F_{1,\,24} = 8.51$, $P = 0.008$). Species that had higher fungal damage found in the center of the monoculture main plot showed a less positive response to species richness under fungicide application (Fig. 2a, Fig. S2). The species whose response to species richness was reduced by fungicide were the ones with thin leaves (high SLA; Fig. 3a; $r = -0.55$, $n = 10$, $P = 0.07$ in site B) and high nitrogen concentrations (low leaf C:N; Fig. 3b C/N: $r = 0.64$, $n = 10$, $P = 0.026$ in site B). Increases in leaf economic value (higher SLA or lower C/N) were correlated with increases in monoculture leaf pathogen load, especially in site B (SLA: $r = 0.53$, $n = 10$, $p = 0.077$; C/N: $r = -0.81$, $n = 10$, $P = 0.001$). Note that the reference effect in monoculture was measured in the main plot's center, i.e. from data which was not used to calculate the diversity effect. In other words, the negative correlation is not merely the result of an autocorrelation of intercept and slope in the regression.

The modification of species-level diversity effects by insecticide application was unrelated to insect damage observed in monocultures ($F_{1,87} = 2.87$, $P = 0.1$) or any other leaf functional traits (Fig. 2b). We didn't find any correlation between herbivore damage with leaf functional traits either (SLA: $r = -0.14$, $n = 10$, $P = 0.66$; C/N: $r = 0.024$, $n = 10$, $P = 0.94$).

Mechanisms

In our study design, all mixtures had corresponding communities with half the species richness that, when joined, represented the full species set of the mixture. Compared to control conditions, fungicide application resulted in significantly fewer mixtures that overyielded relative to their component halves (χ^2-test, $P = 0.030$; Fig. 4a, b). No corresponding effect was found for the insecticide application.

When decomposing overyielding relative to monocultures using Loreau and Hector's additive partitioning scheme, we found a significant decrease of complementarity effect when fungicide was applied (Fig. 5, $F_{1,66} = 0.91$, $P = 0.34$ after 17 months; $F_{1,66} = 6.43$, $P = 0.01$ after 29 months). A similar but statistically insignificant trend was found for insecticide application (Fig. 5, $F_{1,66} = 0.39$, $P = 0.53$ after 17 months; $F_{1,66} = 2.05$, $P = 0.16$ after 29 months). No insecticide or fungicide effects were found on selection effects; overall, these were not significantly different from zero (-0.96 ± 1.54 in control plots; -0.066 ± 0.34 in fungicide plots, 0.11 ± 0.25 in insecticide plots in 2015; -1.05 ± 0.72 in control plots; 0.12 ± 0.36 in fungicide plots, -0.44 ± 0.37 in insecticide plots in 2016).

DISCUSSION

Here we explored the effects of species richness on stand tree volume (or basal area) in response to herbivore and fungal pathogen release. We found positive tree species richness effects on stand productivity under control conditions, but these were greatly reduced and in fact vanished when fungicide was applied. This suggests that foliar fungal pathogens, but not insect herbivores, are one of the major determinants of the diversity–productivity relationship in our study system. These findings indicate that negative density-dependent effects underlie to observed community-level BEF relationship in subtropical forest, which is in-line with experimental model studies with grassland species (Klironomos 2002; Maron *et al.* 2011; Schnitzer *et al.* 2011).

Hantsch (2014) found that most foliar fungal pathogens are highly host-specific. Their passive mode of dispersal makes them dependent on the density of suitable hosts in their surroundings (Hantsch *et al.* 2014). However, when diversity increases, the probability of an individual plant growing near a conspecific individual decreases, resulting in a lower probability of infection. Thus, when eliminating the pathogens, for example by fungicide application, the effect of such enemy release on tree growth is larger at low than at high diversity.

This mechanism is corroborated by our observation that complementarity effects decreased under fungicide application. Specifically, our findings suggest that fungicide application eliminated positive effects of complementary foliar pathogen niches among tree species. Thus, tree community diversity may not only promote productivity by increasing niches for resources but also for trophic interactions.

In our study, stand tree volume of highly diverse communities was reduced by fungicide relative to untreated control plots; while this effect was not statistically significant, it is conceivable that fungicide application also had general detrimental effects on tree communities, for example by direct toxic effects of by affecting beneficial leaf micro-organisms (Laforest-Lapointe *et al.* 2017). An alternative explanation may be related to the fact that leaf area losses due to insect herbivory and leaf fungi were correlated in control plots ($r = 0.45$, $n = 25$, $p = 0.02$). Eliminating leaf fungal pathogens by fungicide application may have promoted herbivore activity, and possibly more so at higher tree species richness (Schuldt *et al.* 2017), which may have cause negative effects of fungicide application on tree volume growth.

The contrasting effects from the exclusion of fungal pathogen and insect herbivores in our study suggest that different mechanisms have been at play for both groups of enemies. The absence of insecticide effects could potentially be explained by the absence of herbivory-effects on tree growth. However, we consider this unlikely given the rather high damage levels we observed in these subtropical tree communities, and the importance of herbivory in controlling primary production in subtropical systems in general. An alternative explanation would be that insect herbivore populations, unlike the ones of leaf fungi, were not limited by host densities. In forest stands in a nearby nature reserve, we in fact found that herbivore damage increased with tree species richness, suggesting that a more diverse community supported a larger or at least a more active herbivore community, possibly because many herbivores easily move from tree to tree and therefore can benefit from better nutrition due to dietary mixing (Brezzi *et al.* 2017). In plots of BEF-China experiment that are not part of the analysis presented here, we found evidence that higher species richness (Schuldt *et al.* 2017) and higher genetic diversity within species (Hahn *et al.* 2017) resulted in higher herbivory levels, supporting the same reasoning. Taken together, these observations suggest that leaf fungi benefitted from higher host densities in monoculture, and their suppression therefore lead to a stronger enemy release at low diversity and a resulting weakening of species richness effects on tree growth. In contrast, insect herbivores likely did not show such an effect, or even benefitted from more diverse communities, resulting in no effect on tree growth when they were excluded.

The experimental removal of arthropods and soil and leaf fungi promoted biodiversity effects on plant growth in the Cedar Creek biodiversity experiment (Seabloom *et al.* 2017). This finding contrasts the effect we found for fungal exclusion in our system, but is in-line with the reasoning that more diverse communities could support a larger community of enemies. Also, the Cedar Creek experiment has been running for over ten years; recent studies have indicated that rapid evolutionary changes can occur through such short period by selecting genotypes that perform best in the particular diversity environment (Zuppinger-Dingley *et al.* 2014). It thus appears that grassland plants in low-diversity plots were selected for effective defense, and that the effect of enemy release thus was smaller in this study.

Species within communities differed with respect to enemy removal. In our study, many species co-occurred due to the nature of our experimental design, i.e. they were not randomly matched in the different experimental communities. Separating treatment-effects on the species from indirect effects via competition with co-occurring species is difficult. Nevertheless, we found for both fungicide and insecticide treatments that, pesticide effects on diversity effects became stronger (with more negative slopes) when larger reductions of growth were observed in monoculture (Fig. S2, S3). While this in part may be related to a correlation of parameters due to the use of monoculture data for both estimates, it is remarkable that diversity effects also were related to leaf economic traits (Wright *et al.* 2004) that were measured in the center of the main plot, i.e. on trees different from the ones that were used to determine the species-richness effect. Together this promotes the idea that species that were more susceptible to enemies benefitted more from enemy removal and therefore contributed more to community-level diversity effect under natural conditions.

In conclusion, our study suggests that in subtropical forest complementarity for enemy niches, in particular for leaf pathogens, promotes community-level diversity effects.

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Figures

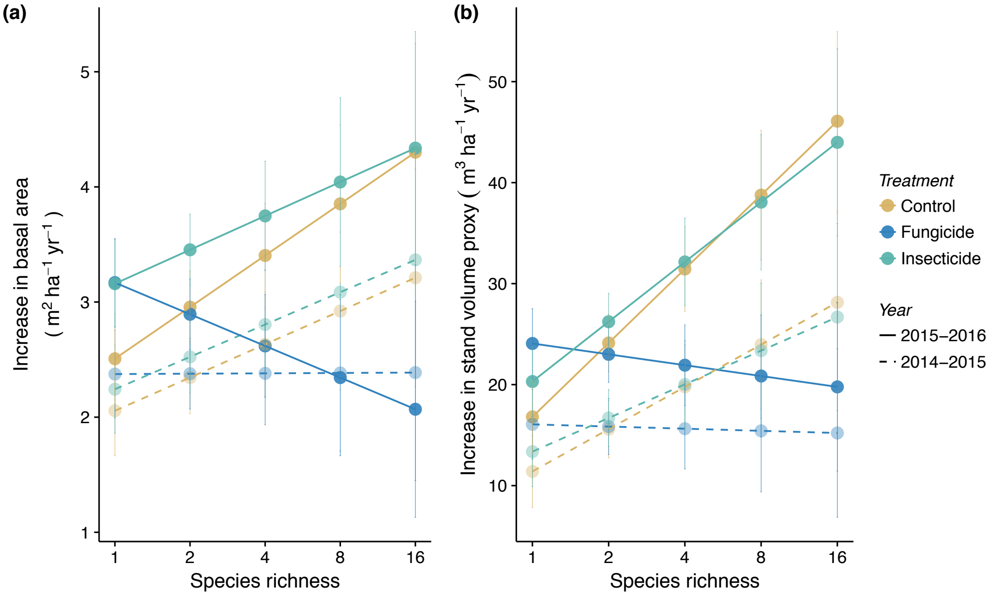


Figure 1 Effects of insecticide and fungicide on the relationship between biodiversity and productivity (change of basal area (a), change of stand volume proxy (b)). The figure shows predicted means and standard errors based on fitted mixed models. Pathogen release benefit more in monocultures, while herbivore release increase productivity overall.

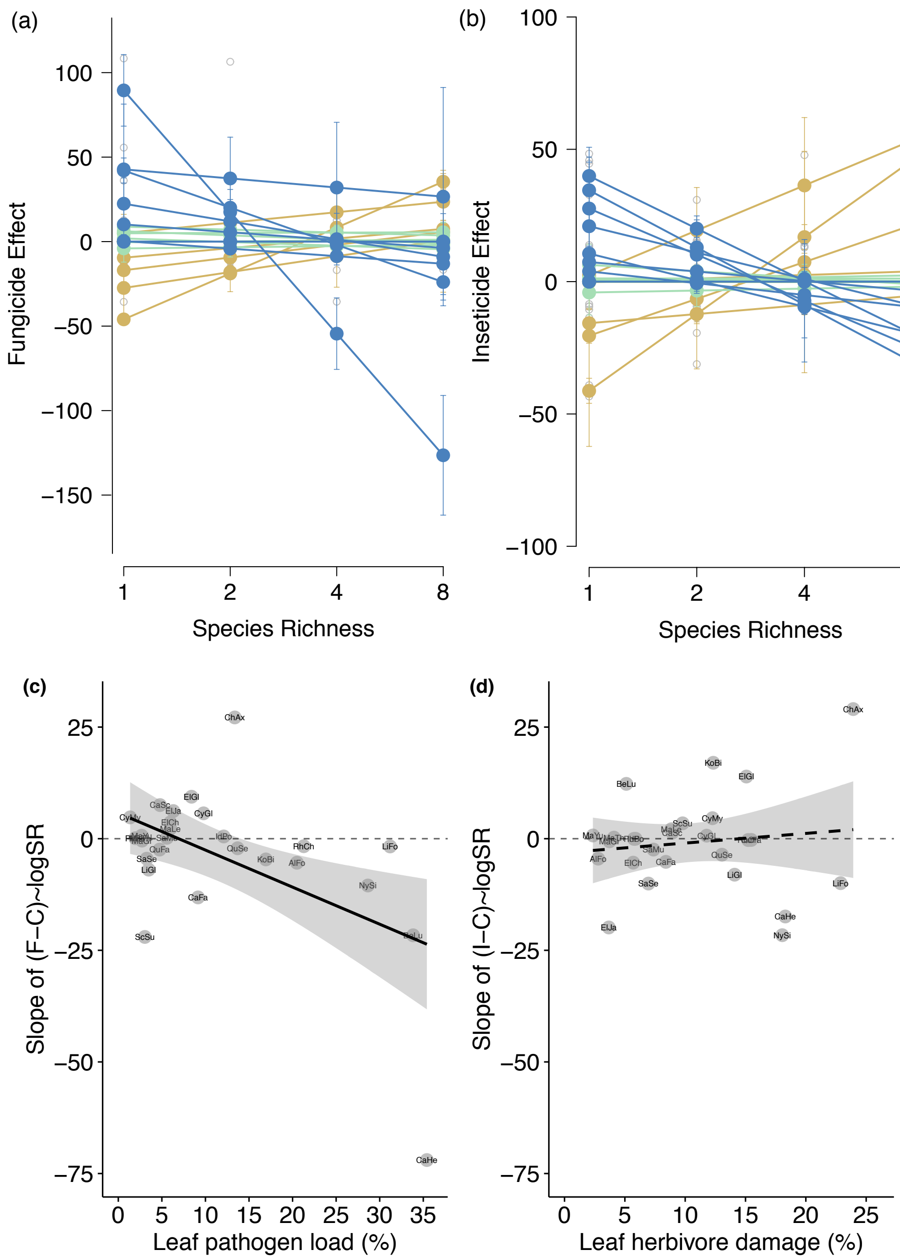


Figure 2 Relationships between species richness and fungicide effects (a) or insecticide effects (b) for different species. The unit of the pesticide effects is $m^3ha^{-1}yr^{-2}$. The fungicide effects were differences of specific species population volume increase from 2015 to 2016 between fungicide treatment subplots and control subplots. Same went for the insecticide effects. Blue color dots and lines with negative slopes represent those species benefit more from pest exclusion in lower diversity levels than higher diversity levels, while yellow color shows opposite species group. The green color dots and lines showed species group that didn't differ for different diversity levels in reacting to pesticide exclusion. The slopes in figure (a) can be explained by leaf pathogen load (c), but slopes in figure (b) couldn't be explained by leaf herbivore damage (d).

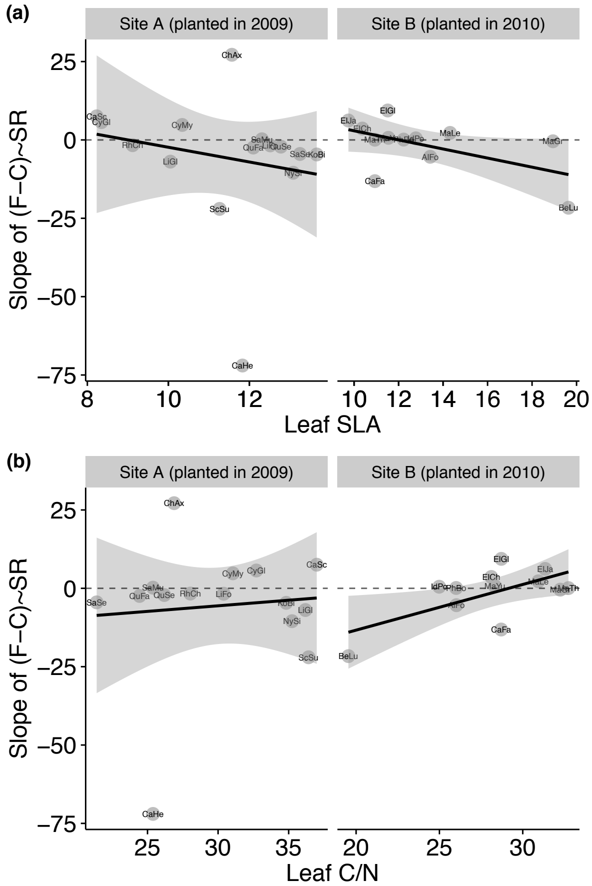


Figure 3 Relationship between species leaf SLA (b) and CN (c) and fungicide effect on the BEF relationship (coefficient of species richness and fungicide effects on diversity effects).

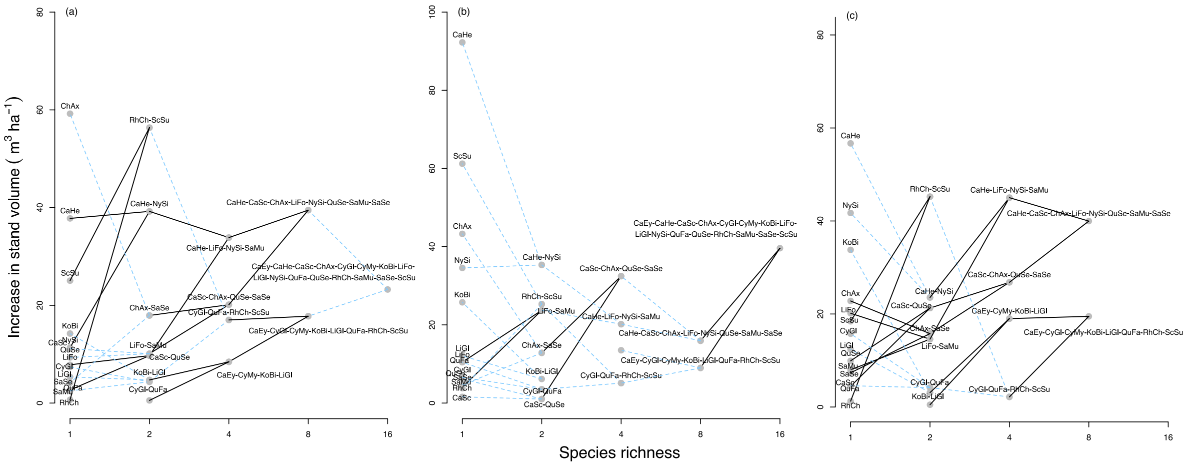


Figure 4 Community stand volume increase from 2014 to 2015 change with diversity gradient in site A for control subplot (a), fungicide subplot (b) and insecticide subplot (c). Solid lines represent overyielding, while dashed lines represent underyielding. Community composition for each plot was shown here. Species full name can be seen from supplementary material Table S1.

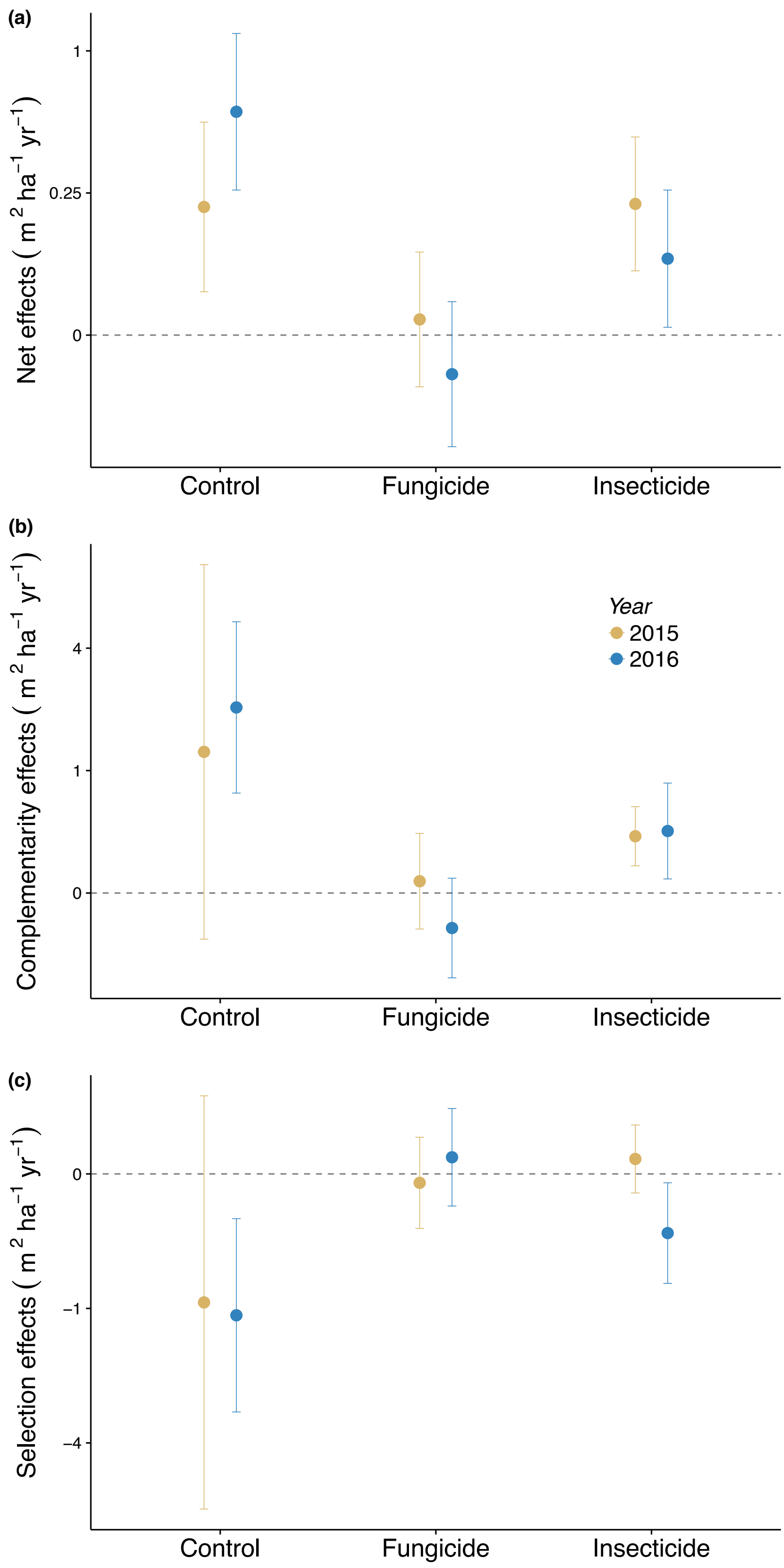


Figure 5 Net effect (a), complementarity effect (b) and selection effect (c) on the stand tree basal area increase in 2015 and in 2016 with different treatments. The ordinate is square-root scaled to reflect the quadratic nature of diversity effects.

Tables

Table 1 Difference between border area and central area for the diversity effect on tree volume increment.

	df	ddf	*F*	*P*
(Intercept)	1	46.30	76.38	0.00
site	1	49.90	6.11	0.02
logSR	1	50.30	6.21	0.02
plot type	1	51.40	2.01	0.16
logSR:plot type	1	53.50	1.22	0.28
Variance components		component	std.error	z.ratio
comp (site A)		290.96	122.17	2.38
comp (site B)		30.43	61.77	0.49
comp:Year		114.66	28.67	4.00
comp:border		163.85	40.48	4.05
Residual		63.50	12.75	4.98

Table 2 Effect of heterotroph removals and diversity on tree volume increment.

	df	ddf	*F*	*P*
(Intercept)	1	50.40	77.15	<0.001
site	1	52.30	6.69	0.01
year	1	46.70	30.03	<0.001
logSR	1	55.90	1.99	0.16
fungicide (contrast within treatment)	1	102.40	0.00	0.98
residual treatment effect	1	102.30	0.46	0.50
year:logSR	1	53.10	0.87	0.36
year:fundicide	1	101.70	0.37	0.54
year:treatment	1	101.40	0.25	0.62
logSR:fungicide	1	111.70	6.90	0.01
logSR:treatment	1	106.20	0.20	0.66
year:logSR:fungicide	1	112.20	4.19	0.04
year:logSR:treatment	1	106.70	0.06	0.81
Variance components		component	std.error	z.ratio
comp (site A)		249.67	94.53	2.64
comp (site B)		117.54	53.29	2.21
comp:year (site A)		78.92	28.31	2.79
comp:year (site B)		21.81	12.73	1.71
comp:treatment (site A)		141.63	33.35	4.25
comp:treatment (site B)		126.50	33.03	3.83
Residual		59.18	8.43	7.02

Note:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table.

Abbreviations: comp = Species composition in each plot; df = nominator degree of freedom; ddf = denominator degree of freedom; logSR = $\log_2$(tree species richness). *F* and *P* indicate F-ratios and the P-values of the significance test.

SUPPLEMENTARY MATERIAL

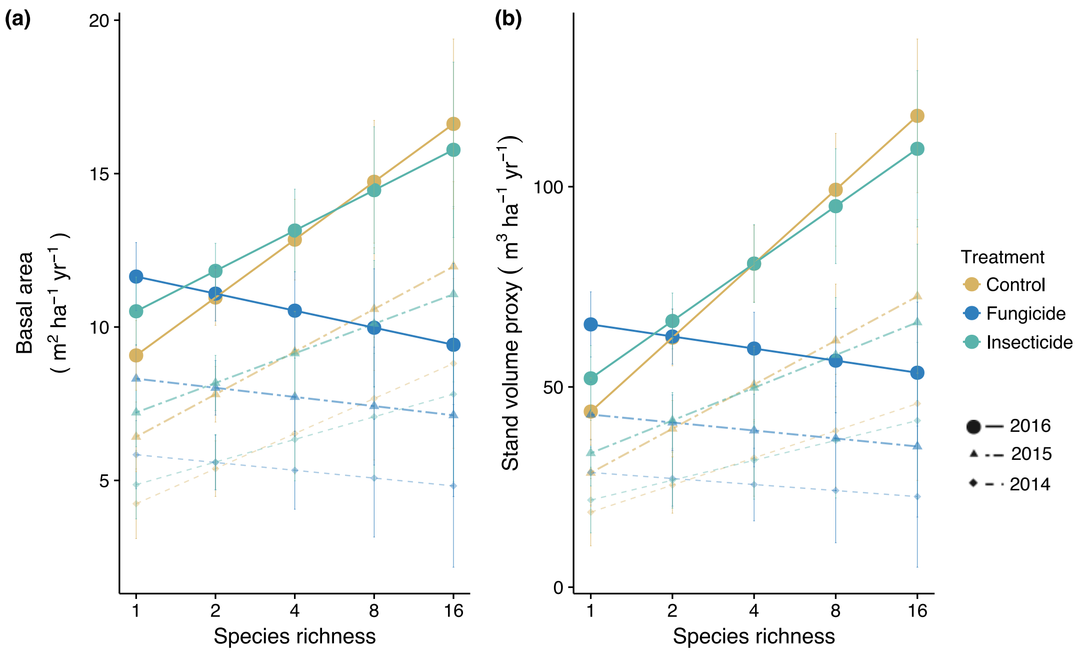
The following supplementary material is available for this article:

Figure S1 Effects of insecticide and fungicide on the relationship between biodiversity and producticity (basal area (a), stand volume proxy (b)). The figure shows predicted means and standard errors based on fitted mixed models.

Figure S2 Fungicide treatments effects on different species monoculture plantations (a) and coefficients of the relationship between species richness and fungicide treatment (b). Negative slope means fungicide treatments benefit more in low diversity gradients than higher levels.

Figure S3 Insecticide treatments effects on different species monoculture plantations (a) and coefficients of the relationship between species richness and insecticide treatment (b). Negative slope means insecticide treatments benefit more in low diversity gradients than higher levels.

Table S1 Species list in this experiment according to the Flora of China



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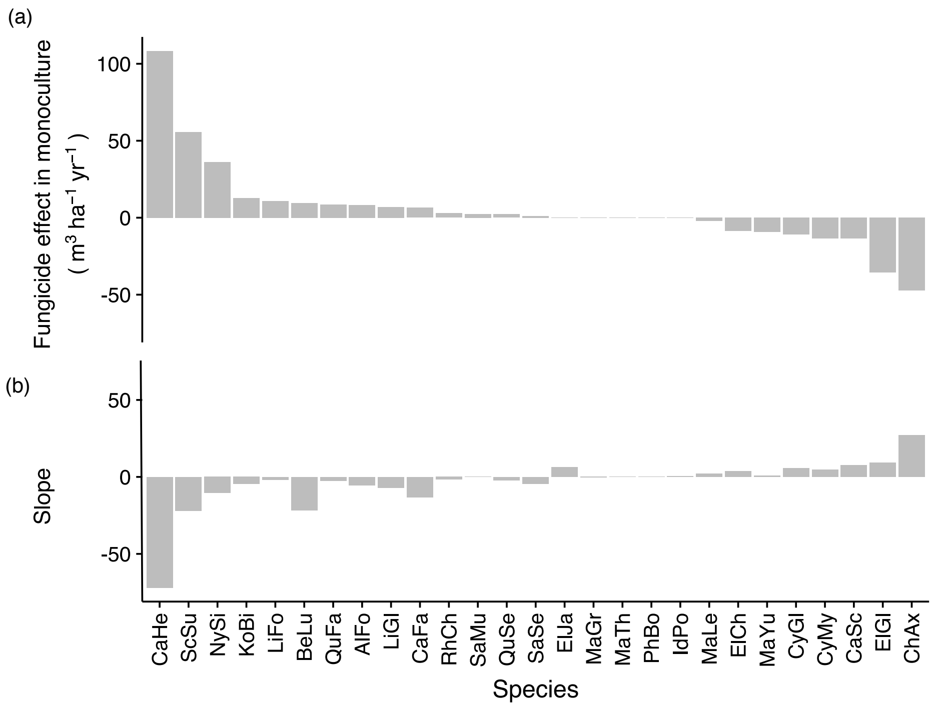

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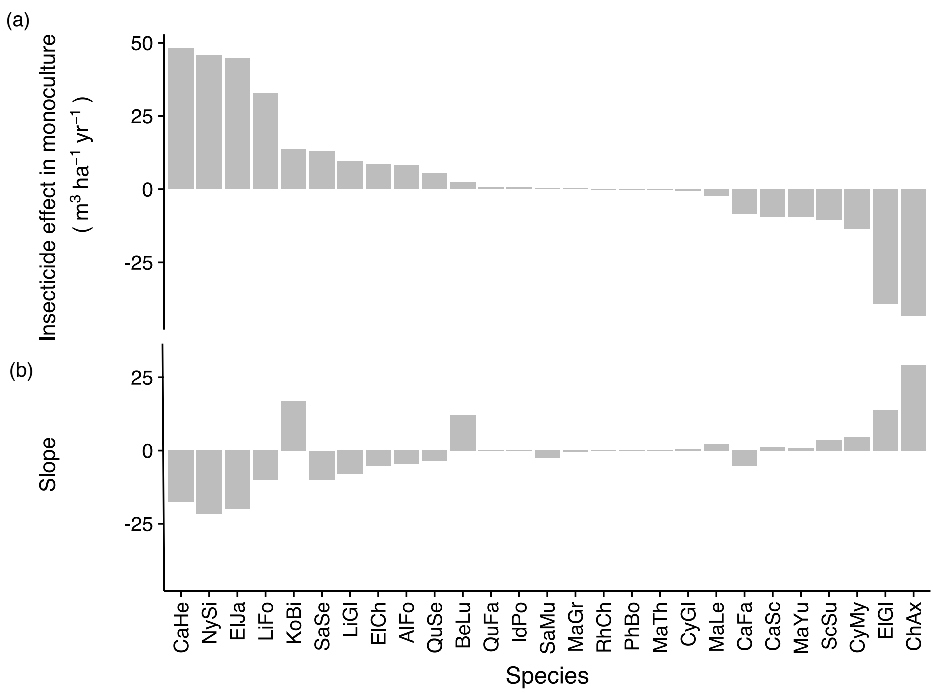

Figure S3 Insecticide treatments effects on different species monoculture plantations (a) and coefficients of the relationship between species richness and insecticide treatment (b). Negative slope means insecticide treatments benefit more in low diversity gradients than higher levels.

Table S1 Species list in this experiment according to the Flora of China (http://www.efloras.org and http://frps.eflora.cn).

Species	Short name	Site	Type
Ailanthus altissima (Miller) Swingle	AiAl	B	Deciduous
Alniphyllum fortunei (Hemsley) Makino	AlFo	B	Deciduous
Betula luminifera H. Winkler in Engler	BeLu	B	Deciduous
Castanea henryi (Skan) Rehd. et Wils.	CaHe	A	Deciduous
Castanopsis eyrei (Champion ex Bentham) Tutcher	CaEy	A	Evergreen
Castanopsis fargesii Franchet	CaFa	B	Evergreen
Castanopsis sclerophylla (Lindley & Paxton) Schottky	CaSc	A	Evergreen
Celtis biondii Pampanini	CeBi	B	Deciduous
Choerospondias axillaris (Roxb.) Burtt et Hill	ChAx	A	Deciduous
Cyclobalanopsis glauca (Thunberg) Oersted	CyGl	A	Evergreen
Cyclobalanopsis myrsinifolia (Blume) Oersted	CyMy	A	Evergreen
Elaeocarpus chinensis (Gardner & Champion) J. D. Hooker ex Bentham	ElCh	B	Evergreen
Elaeocarpus glabripetalus Merrill	ElGl	B	Evergreen
Elaeocarpus japonicus Siebold & Zuccarini	ElJa	B	Evergreen
Idesia polycarpa Maximowicz	IdPo	B	Deciduous
Koelreuteria bipinnata Franch.	KoBi	A	Deciduous
Liquidambar formosana Hance	LiFo	A	Deciduous
Lithocarpus glaber (Thunb.) Nakai	LiGl	A	Evergreen
Machilus grijsii Hance	MaGr	B	Evergreen
Machilus leptophylla Handel-Mazzetti	MaLe	B	Evergreen
Machilus thunbergii Siebold & Zuccarini	MaTh	B	Evergreen
Manglietia fordiana Oliv. in Hook (Old name: *Manglietia yuyuanensis*)	MaYu	B	Evergreen
Meliosma flexuosa Pampanini	MeFl	B	Deciduous
Nyssa sinensis Oliver	NySi	A	Deciduous
Phoebe bournei (Hemsley) Yen C. Yang	PhBo	B	Evergreen
Quercus fabri Hance	QuFa	A	Deciduous
Quercus phillyreoides A. Gray	QuPh	B	Evergreen
Quercus serrata Murray	QuSe	A	Deciduous
Rhus chinensis Mill.	RhCh	A	Deciduous
Sapindus abruptus Loureiro (Old name: *Sapindus mukorossi*)	SaMu	A	Deciduous
Schima superba Gardn. et Champ.	ScSu	A	Evergreen
Triadica sebifera (Linnaeus) Small (Old name: *Sapium sebiferum*)	SaSe	A	Deciduous

Chapter 3

Overyielding of litter production in a large subtropical forest biodiversity experiment

(Formatted for submission to *Forest Ecosystems*)

Overyielding of litter production in a large subtropical forest biodiversity experiment

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ABSTRACT

The production of aboveground litter is an important process in the turnover of primary production. Litterfall links above- and belowground processes by transferring organic material that then becomes available to soil heterotrophs, and by enabling nutrient (re-) cycling. Several studies have demonstrated that plant primary productivity increases with plant species richness, but relatively little is known about effects on litter fluxes, and the available studies generally have been conducted in ecosystems other than species-rich forests. We set up an experiment in BEF-China, a large platform for forest-biodiversity research, to study the relationship between planted tree species richness ranging from 1–16 species and litter production. We found a positive effect of tree species richness on yearly litter production; and this biodiversity effect increased with time. In addition, we found a positive correlation between litter overyielding and vertical crown complementarity among tree species, suggesting a relationship between complementary light use and litter production in species-rich forests of the study area. Different species had different temporal dynamics of litterfall, which led to a more or less constant litter supply in species-rich stands over the whole year; this in turn may positively affect mineralization and subsequent tree growth.

Keywords: BEF-China; complementarity effects; litterfall; overyielding; tree species richness

1. Introduction

Forests, especially in subtropical and tropical regions, are important habitats that harbour one third of the terrestrial higher plant species (FAO, 2010). Forests provide important ecosystem services to humans such as the production of timber and fiber, the provisioning of energy sources, opportunities for recreation and regulating functions for the local and global climate via carbon sequestration and transpiration. At the same time, there is growing evidence that the loss of biodiversity may impair the functioning of ecosystems, and therefore also their provisioning of ecosystem services.

Researchers already dug deep into the role of biodiversity on ecosystem functioning in grassland ecosystems (Tilman *et al.*, 2014). However, experimental biodiversity–ecosystem functioning (BEF) research in forest ecosystems is still at its beginning and evidence about effects and underlying mechanisms is largely lacking because of the long time-spans involved, space requirements and measurement complexity (Clarke *et al.*, 2017). Scientists had long debates regarding the role of biodiversity for ecosystem functioning (Kaiser, 2000). Most of them currently believe in a strong link, arguing that forests ecosystems cannot cope with stresses and climate change if the diversity of the system is reduced too much (Liang *et al.*, 2016). Others suggest neutral processes may be important and diffuse coevolution may result in niche convergence toward generalist strategies in forest (Hubbell, 2006, Wang *et al.*, 2016). Some argued that there are many redundant species in highly diverse forests and removal of those species would not impair ecosystem functioning (Lawton *et al.*, 1994).

Litter production plays a crucial role in forest ecosystems as the link between above- and belowground process. Physically, tree litter creates a cover enhancing soil moisture and stabilizing soil temperature (Thompson, 2011). Chemically, litter quantity and quality determine decomposition processes and nutrient mineralisation (Manzoni *et al.*, 2008), which in turn provide nutrients for future plant growth. Litter production can be an important way for trees to interact with each other by sharing information and resources (Sapijanskas *et al.*, 2013). Depending on the amount of nutrients returned and shared with neighbours, trees can have competitive and facilitative interactions. Researchers in temperate stands showed that Norway spruce (*Picea abies*) benefited from a continuous “facilitation” by European beech (*Fagus sylvatica*), which, they argued, improved water and nutrient supply by beech litter translocation, improved decomposition, higher turnover of mixed litter and humus activation (Pretzsch *et al.*, 2010). In mixed communities, with niche differentiation of nutrient uptake between species, resource sharing via litter may increase tree growth at the stand level. Thus, it would be important to know whether multi-species communities with inter-specific interactions will have different litter production than monocultures.

Direct measurements of litterfall over multiple years in forests stands of different species richness have rarely been done. One comparative study found that litter quantity as well as litter quality increased with tree species richness in a natural subtropical forest after accounting for effects of forest age (Huang *et al.*, 2017). However, comparative studies in natural forests can only establish correlative evidence for a relationship and experimental studies are required to determine causality. Such experiments have only recently been established and in the only one in which litter production was measured, litter production was higher in mixtures of three species than in monocultures or mixtures of six species (Scherer-Lorenzen *et al.,* 2007).

To test the relationship between tree species richness and litter production across a larger diversity gradient, we used the biodiversity experiment set up in BEF-China (Bruelheide *et al.,* 2014) with richness levels of 1, 2, 4, 8 and 16 species and measured litterfall in 101 plots monthly during the growing season in 2014, 2015 and monthly around the whole year in 2016. We used the data to test the following three hypotheses: 1) litter production increases with tree species richness at the community level and this relationship increases over time; 2) overyielding in mixtures can be related to vertical crown complementarity between species; 3) different species shed litter at different times of the year, thus leading to a more constant litter input to the ecosystem over the year in more species-rich experimental forest stands.

2. Methods

2.1. Experimental design

The present study was carried out as part of a large forest biodiversity experiment, "BEF-China", which was established near the village Xingangshan in Jiangxi Province in south-east China (29°08′–29°11′ N, 117°90′–117°93′ E). The climate at the site is subtropical, with a mean annual temperature of 17 ℃ and a mean annual precipitation of 1800 mm (years 1971–2000) (Yang *et al.*, 2013). The experiment consists of two sites (A and B) that are 5 km apart from each other and each cover an area of ca. 20 ha. The overall experiment consists of more than 500 plots of 25.8 × 25.8 m in horizontal projection, which equals the Chinese area unit of 1 mu. Each plot was planted with 400 trees that were arranged on a rectangular 20 × 20 grid with 1.29 m distance between neighbors. In mixed species communities, species were randomly distributed with equal numbers of individuals. A detailed description of the experimental set up can be found in (Bruelheide *et al.*, 2014).

For the present study, we used 124 plots with 1, 2, 4, 8 or 16 species. To construct communities with different species compositions, we arranged the 16 species that were common in the near-natural forests surrounding the experiment into random sequence. This set of species was then repeatedly divided into halves, halves of halves, and so on until 16 monocultures were obtained. This procedure was applied separately at the two experimental sites, with distinct, non-overlapping sets of species. Our experimental design ensured that all species were equally represented at all diversity levels. In total, there were 62 unique community compositions: two 16-species mixtures, four 8-species mixtures, eight 4-species mixtures, 16 2-species mixtures, and 32 monocultures. Each unique species composition was established in two separate plots that were at random positions within the site. One of the two plots was part of cluster that included three additional plots with the same composition but additional experimental treatments, but these extra plots and treatments were not considered in the present study.

We installed three litter traps in the central area of each plot (Fig. 1) in March 2014 at site A and in March 2015 at site B. Litter traps were made of nylon nets (1 mm mesh) placed over a PVC frame with a horizontal trapping area of 0.75 × 0.75 m. The litter traps were placed under the tree canopy at the height from 1 to 1.5 m above ground, depending on the height of the tree canopy. No traps were installed in six plots at site A and 17 plots at site B because average tree height was lower than 1 m at the time the traps were set up. In total, 56 plots at site A and 45 plots at site B were equipped with traps.

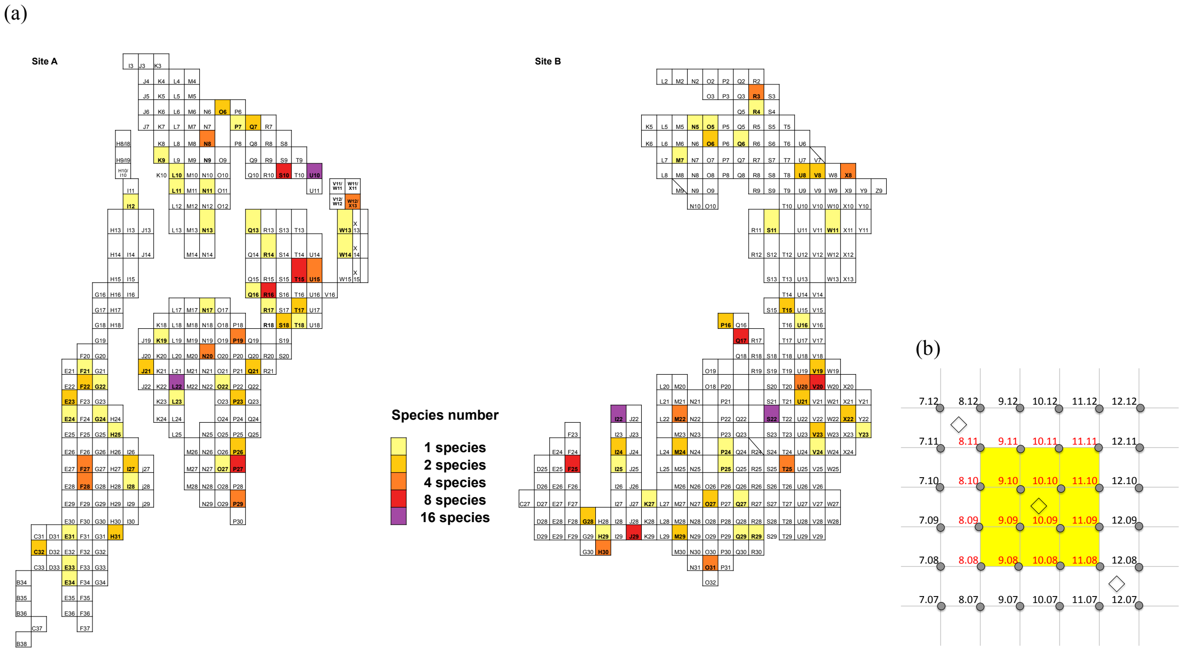

Fig. 1 Map of litter-trap plots at sites A (left) and B (right) (a). Each square represents a plot. The plots filled with color were installed litter traps. Position of the litter traps (diamond shapes) within a plot was shown on the right (b). The yellow area indicates the plot's central 16 trees. Numbers indicate individual tree positions with column (07–12) and row (07–12) coordinates.

2.2. Litter collection

Litter collection started in September 2014 at site A and September 2015 at site B. The litter traps were emptied once per month. We sorted litter collected from September to December 2014 into leaf litter and non-leaf litter (fine branches ≤2.5 cm in diameter, bark, reproductive structures, animal detritus, and other unidentified fine litter). We found that only about 5% of the total was non-leaf litter and therefore did no longer separate litter after that period. Litter amounts were very low in February and June 2016, and we therefore collected it together with the litter trapped in the next month. All litter samples were weighed after oven-drying at 60 °C for 48 hours.

Monthly litter production was calculated by first determining daily litter production as ratio of litter amounts recovered and collection period in days and then adding values for each particular month.

In addition to litter samples, we measured the basal diameter of all surviving central trees in each plot at 5 cm of the central 16 individuals in the core area of the plot to calculated stand basal area. Furthermore, we determined the vertical dimensions of all tree crowns by measuring crown start and tip with a measuring pole. Lowest crown height and tree height of the central 16 trees were also measured for crown niche dissimilarity measurements.

2.3. Vertical crown complementarity measure between species

Considering the vertical extent of tree crowns as a trait-based niche measure (Roscher *et al.*, 2015), vertical crown complementarity between species can be calculated using proportional dissimilarity (Schoener, 1970). We calculated the crown niche for each species using the average heights of crown starts and tips in monocultures. We expected that larger proportional dissimilarity as indication of larger vertical crown complementarity between species in a multi-species plot would be related to higher efficiency of light use by the stand, which in turn could lead to more litter production. We used monoculture values to avoid circularity. In particular, species may adjust their crowns in mixtures as a consequence of light competition (Niklaus *et al.*, 2017, Williams *et al.*, 2017), whereas here we wanted to test if a-priori differences between species were related to litter production as an exemplary ecosystem function. Proportional dissimilarity was calculated as follows (Colwell *et al.*, 1971, Schoener, 1970).

$$PDS_{A,B} = \frac{1}{2}|X_A - X_B|$$

X_A is the probability that species A is associated with light resource niche, calculated by dividing species A crown niche (average data from monocultures) by the total A and B niche length. This is the same for X_B. Mean pairwise proportional dissimilarity for a plot was calculated by averaging the PDS of all possible pairs of species.

2.4. Data analyses

The litterfall values from September to November in the years 2014, 2015 and 2016 were summed each year to get the peak-senescing period litter production. Yearly litterfall in 2016 was calculated by adding all litterfall collected that year. To detect biodiversity effects on litterfall, we calculate litterfall overyielding in mixtures by comparing differences of the mixture litter production with the mean values of the corresponding monocultures (Schmid *et al.*, 2008).

We used linear mixed-effects models to test the tree species richness effects on yearly litter production in 2016 (Schmid *et al.*, 2017). Fixed-effects terms included site and species richness, and species composition was used as random-effects term. The model with crown proportional dissimilarity on litterfall overyielding was similar. We analysed biodiversity effects on the peak-senescing period from 2014 to 2016 in site A and from 2015 to 2016 in site B separately. Fixed-effects terms were species richness, year, interaction of year and species richness. Random-effects terms were species composition and the interaction of species composition and year. Pearson correlation analysis was used to get the correlation between plot litterfall and stand basal area. Species richness was $\log_2$ transformed in all the analyses. Litterfall data were squared-root transformed to meet assumptions of variance homogeneity and normality.

3. Results

3.1. Monthly and yearly litter production

In 2016, yearly litter production was 3.32 ± 0.27 Mg ha^{-1} yr^{-1} and 2.51 ± 0.24 Mg ha^{-1} yr^{-1} at sites A and B, respectively, with maximum values of 6.82 Mg ha^{-1} yr^{-1} and 6.49 Mg ha^{-1} yr^{-1}. The intra-annual litterfall dynamics followed a bimodal curve with peaks from April to May and a larger peak from September to November. This pattern was particularly evident in species-rich communities (Fig. 2). Species differed in temporal litterfall patterns (Fig. 2a), with evergreen species peaking in spring (e.g. *Schima superba*) whereas deciduous species peaked in fall (e.g. *Nyssa sinensis, Liquidambar formosana, Alniphyllum fortunei, Choerospondias axillaris*). Interspecific differences in shedding season imply a more constant litterfall rate throughout the year in mixed communities, at least when deciduous and evergreen species grew together.

3.2. Tree biodiversity effects on litter production

Litter production in 16-species mixtures (4.39 ± 1.15 Mg ha^{-1} yr^{-1}) was twice as high as in the average monoculture (2.56 ± 0.27 Mg ha^{-1} yr^{-1}). Litterfall increased with the logarithm of tree species richness (Fig. 1, Table 2, $F_{1, 50.4} = 4.34$, $P = 0.04$).

Peak-senescing period (September to November) litterfall increased through time (Fig. 4, Table 3, $P < 0.001$) by 0.04 ± 0.02 Mg ha^{-1} y^{-1} at site A (period 2014 to 2016) and by 0.07 ± 0.04 Mg ha^{-1} y^{-1} at site B (years 2015 to 2016). Litterfall rates increased more quickly in more species-rich communities, resulting in biodiversity effects. The interaction between year and diversity in site B was marginally significant (Table 3, $F_{(1, 19.4)} = 3.88$, $P = 0.06$), suggesting that the relationship increased from 2015 to 2016. But in site A, the interaction between year and biodiversity was not significant (Fig. 4, Table 3, $F_{(2, 52)} = 1.26$, $P = 0.29$), yet the biodiversity main effect was marginally significant (Table 3, $F_{(1, 27.8)} = 3.46$, $P = 0.07$). By only analysing the total production during this peak season in year 2016 at site A, we found a positive biodiversity effect ($F_{(1, 27.7)} = 4.59$, $P = 0.04$).

3.3. Effects of crown proportional dissimilarity on overyielding of mixtures

Comparing the mixtures with the mean litter production of the monocultures we found significant overyielding. This overyielding effect was marginally positively correlated with crown proportional dissimilarity (Fig. 6, Table 4, $F_{(1, 24.7)} = 3.28$, $P = 0.08$).

Analysis of the overyielding of litterfall in 2016 in mixture communities compared with their relative component monocultures from the broken stick design showed that overyielding happened in 11 out of 15 cases, among which 6 cases were transgressive overyielding, which refers to mixtures outperforming even their 'best' component monoculture (Schmid*, et al.*, 2008) (Fig. 5).

4. Discussion

After eight years of growth annual litter production reached 3.32 ± 0.27 Mg ha^{-1} yr^{-1}, which was similar to that in young stands in nearby natural forest (Huang*, et al.*, 2017). Monthly observations showed that different species varied largely in the seasonal peak of litterfall, which was consistent with other studies (Scherer-Lorenzen *et al.*, 2007). Different shedding season of different species in mixture communities provide relatively constant litter inputs during the whole year, which increases the stability of the ecosystem.

We found a significantly positive biodiversity effect on yearly litter production at site B but not at site A. There was a positive correlation between litterfall and stand basal area at both sites (Fig. 7, Pearson's product-moment correlation $r = 0.76$, $n = 54$, $P < 0.001$ for site A; $r = 0.49$, $n = 43$, $P < 0.001$ for site B). It is possible that diverse communities contribute to higher growth, which in turn may promote litter production. It is unclear if mixed-species communities shed even more leaves than monocultures per stand-level biomass production. LAI measurements in the same plots also showed a positive effect of species richness from 2013 to 2014 (Peng *et al.*, 2017). Thus, it is conceivable that more diverse communities not only produce more leaves but also shed more leaves, which implies faster recycling of nutrients.

Many mixtures showed litter overyielding and even transgressive litter overyielding. This effect is possible caused by the light complementarity effects in mixtures with more diverse crown niches. Some tree plantation studies previously showed that vertical crown complementarity between species can promote overyielding with regard to stand-level productivity (Niklaus*, et al.*, 2017, Williams*, et al.*, 2017). This mechanism can promote more leaf biomass production, which will turn into litterfall in the end.

Higher litter production in mixtures has significant effects on the ecosystem. It is possible that litterfall among tree species is synchronized via unknown mechanisms. A litter manipulation experiment demonstrated the ability of tropical trees to respond to leaf litter nutrient inputs by increasing leaf and litter production within months of litter addition (Wood *et al.*, 2009). Studies in a moist tropical forest showed that increased amounts of litter could promote fine root proliferation to absorb limited nutrients to minimize the potential cost of foraging, resulting in a more effective fine root system on the surface layer (Sayer *et al.*, 2006). Sapijanskas*, et al.*, (2013) highlighted the important role of litter-mediated interactions among trees by showing that litter production by neighbours contributed to overyielding in tropical trees. We provide evidence that mixtures do have higher litter production, which may contribute to overyielding in tree growth.

Funding

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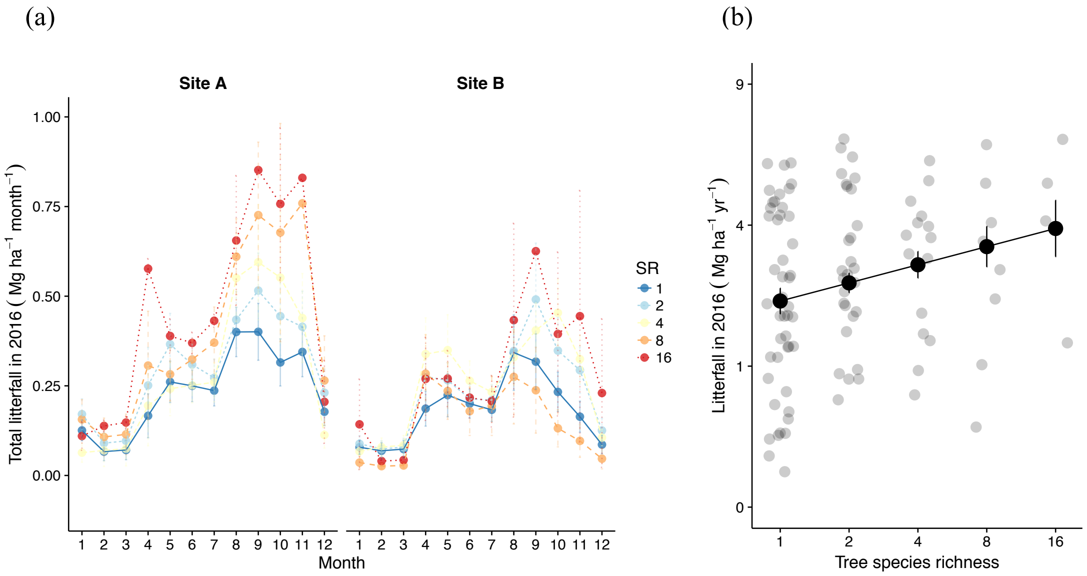

Fig. 2 Temporal dynamics of litterfall across biodiversity gradients in 2016 (a) and biodiversity effects on yearly litter production in 2016 (b). "SR" refers to tree species richness. The lines were fit by a loess method, which uses local averaging as fitting technique. In figure (b), grey dots indicate values for individual plots, whereas black dots and lines are predicted values from the fitted model. Error bars denote ± 1 standard error.

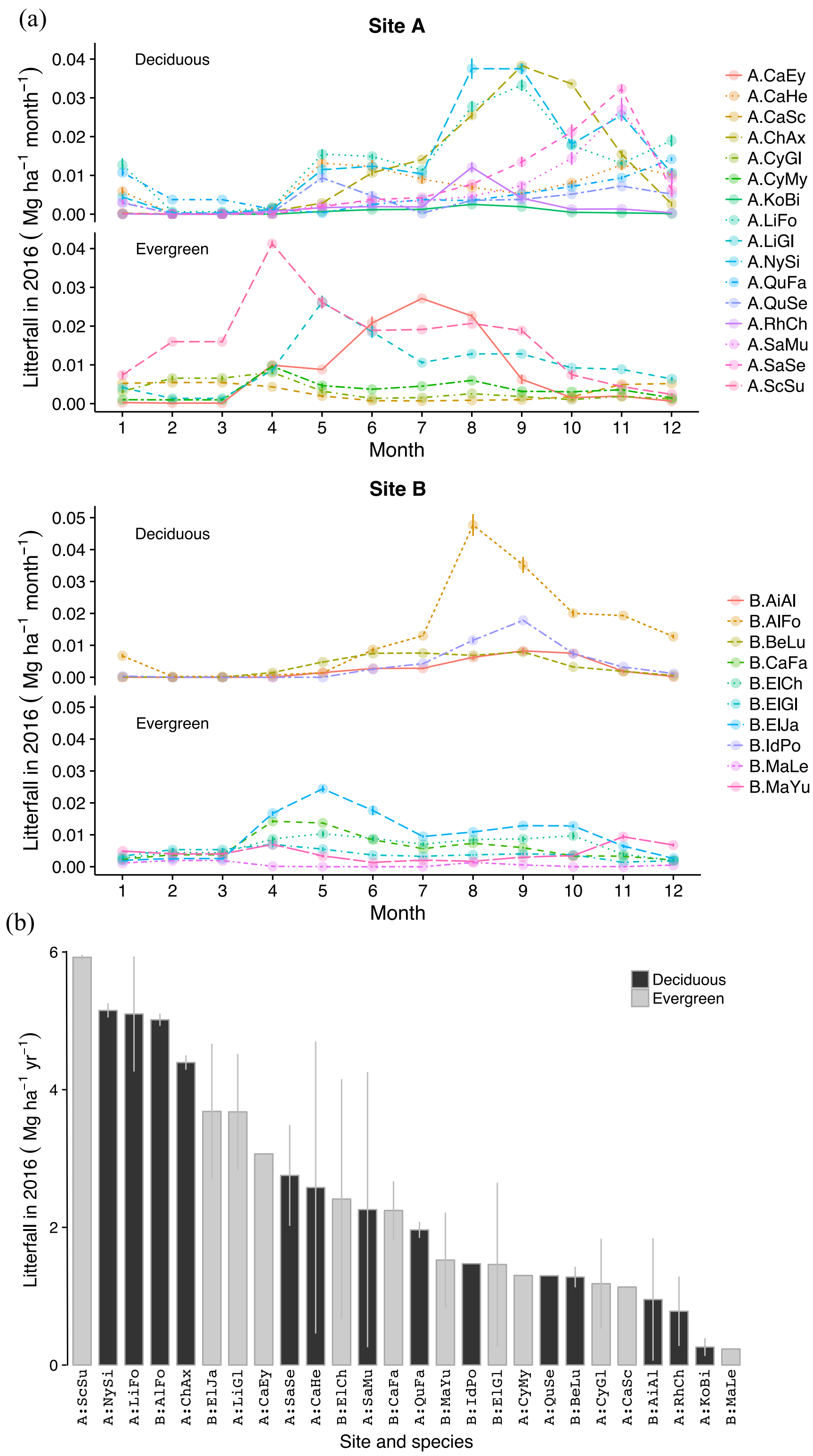

Fig. 3 Temporal dynamics of litterfall in monocultures for different species (a) and yearly litterfall production in 2016 (b). Six monocultures (CeBi, MaGr, MaTh, MeFl, PhBo, QuPh) are excluded because they were still too small to allow us to collect litter. Error bars denote ± 1 standard error (n=2). Full names of the species abbreviations can be seen in Table 1.

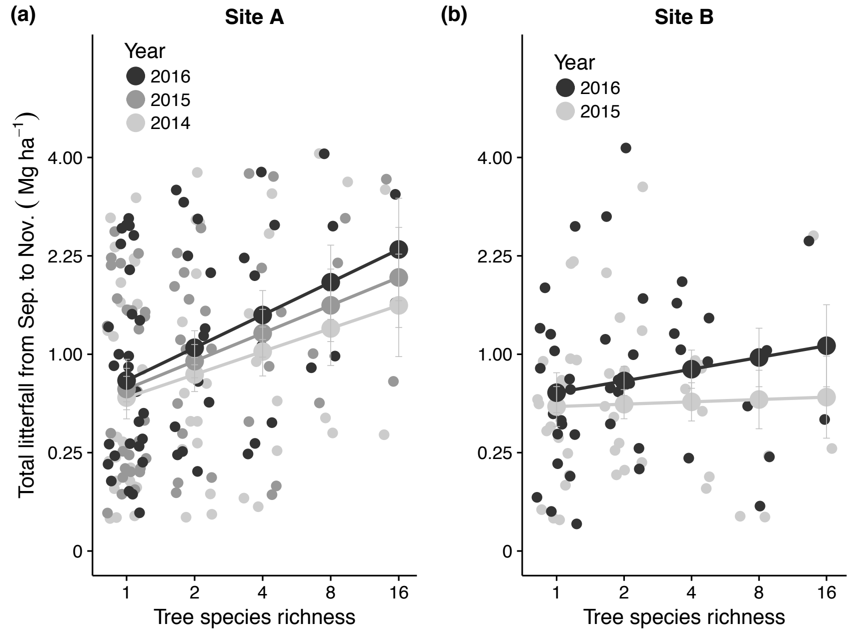

Fig. 4 Difference of the relationship between diversity and litter production among years for site A (a) and site B (b). Regression lines, large dots and error bars (± 1 standard error) are predictions from the fitted mixed-effects models.

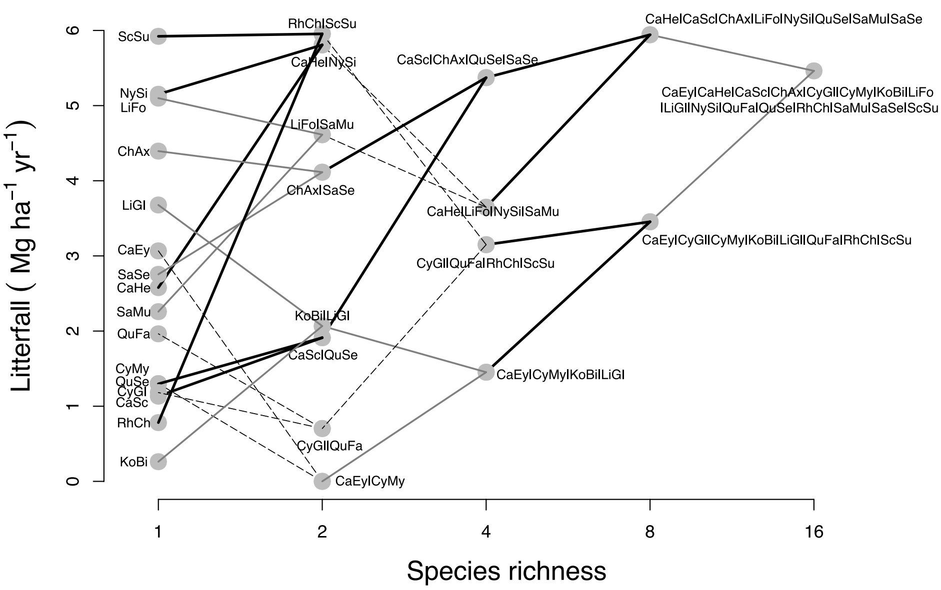

Fig. 5 Overyielding of litterfall production in 2016 in mixtures compared with monocultures from the broken stick design. Data were averaged by species composition. Black solid lines represent transgressive overyielding, grey solid lines represent normal overyielding, while grey dashed lines show the underyielding situations.

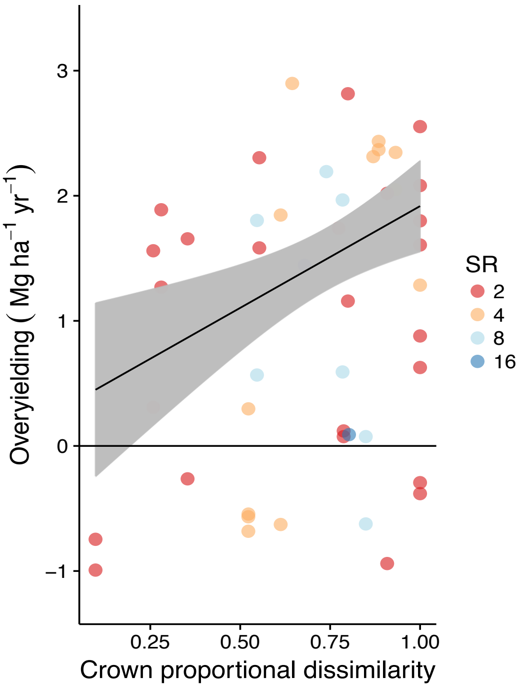

Fig. 6 The effect of crown proportional dissimilarity on litterfall overyielding in 2016. “SR” means tree species richness.

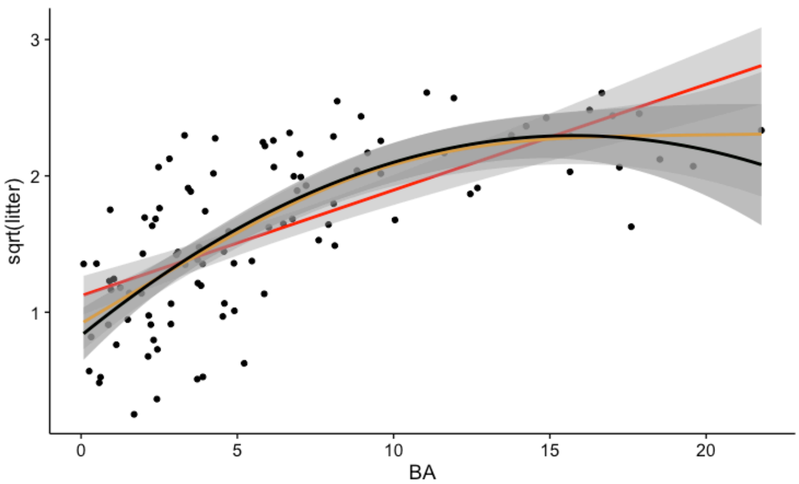

Fig. 7 Relationship between stand basal area and litterfall (square-root transformed). Different lines were fitted with different methods. The black line was fitted using a quadratic function, the orange line with a “gam” method and the red line with simple linear regression.

Table 1 Species list in this experiment according to the Flora of China (http://www.efloras.org and http://frps.eflora.cn).

Species	Short name	Site	Type
Ailanthus altissima (Miller) Swingle	AiAl	B	Deciduous
Alniphyllum fortunei (Hemsley) Makino	AlFo	B	Deciduous
Betula luminifera H. Winkler in Engler	BeLu	B	Deciduous
Castanea henryi (Skan) Rehd. et Wils.	CaHe	A	Deciduous
Castanopsis eyrei (Champion ex Bentham) Tutcher	CaEy	A	Evergreen
Castanopsis fargesii Franchet	CaFa	B	Evergreen
Castanopsis sclerophylla (Lindley & Paxton) Schottky	CaSc	A	Evergreen
Celtis biondii Pampanini	CeBi	B	Deciduous
Choerospondias axillaris (Roxb.) Burtt et Hill	ChAx	A	Deciduous
Cyclobalanopsis glauca (Thunberg) Oersted	CyGl	A	Evergreen
Cyclobalanopsis myrsinifolia (Blume) Oersted	CyMy	A	Evergreen
Elaeocarpus chinensis (Gardner & Champion) J. D. Hooker ex Bentham	ElCh	B	Evergreen
Elaeocarpus glabripetalus Merrill	ElGl	B	Evergreen
Elaeocarpus japonicus Siebold & Zuccarini	ElJa	B	Evergreen
Idesia polycarpa Maximowicz	IdPo	B	Deciduous
Koelreuteria bipinnata Franch.	KoBi	A	Deciduous
Liquidambar formosana Hance	LiFo	A	Deciduous
Lithocarpus glaber (Thunb.) Nakai	LiGl	A	Evergreen
Machilus grijsii Hance	MaGr	B	Evergreen
Machilus leptophylla Handel-Mazzetti	MaLe	B	Evergreen
Machilus thunbergii Siebold & Zuccarini	MaTh	B	Evergreen
Manglietia fordiana Oliv. in Hook (Old name: *Manglietia yuyuanensis*)	MaYu	B	Evergreen
Meliosma flexuosa Pampanini	MeFl	B	Deciduous
Nyssa sinensis Oliver	NySi	A	Deciduous
Phoebe bournei (Hemsley) Yen C. Yang	PhBo	B	Evergreen
Quercus fabri Hance	QuFa	A	Deciduous
Quercus phillyreoides A. Gray	QuPh	B	Evergreen
Quercus serrata Murray	QuSe	A	Deciduous
Rhus chinensis Mill.	RhCh	A	Deciduous
Sapindus abruptus Loureiro (Old name: *Sapindus mukorossi*)	SaMu	A	Deciduous
Schima superba Gardn. et Champ.	ScSu	A	Evergreen
Triadica sebifera (Linnaeus) Small (Old name: *Sapium sebiferum*)	SaSe	A	Deciduous

Table 2 Summary statistics from mixed-effects models for tree species richness effects on yearly litter production in 2016.

	df	ddf	*F*	*P*
Intercept	1	52.0	536.10	<0.001
Site	1	52.2	2.58	0.11
LogSR	1	50.4	4.34	0.04
Variance components		Component	Standard error	z.ratio
Composition		0.16	0.05	2.84
Residual		0.19	0.04	4.86

Table 3 Summary statistics from mixed-effects models for tree species richness effects on peak-senescing period litter production (Sep. to Nov.) for two sites.

Site A	df	ddf	*F*	*P*
Intercept	1	28	127.1	0.000
logSR	1	27.9	3.482	0.073
Year	1	26.9	12.11	0.002
logSR:year	1	26.3	2.113	0.158
Variance components		Component	Standard error	z.ratio
Compsition		0.19	0.06	3.483
Compsition:year		-0.01	0.00	-2.528
Residual		0.08	0.01	7.430
Site B	df	ddf	*F*	*P*
Intercept	1	22.9	123.20	<0.001
LogSR	1	22.4	0.30	0.587
Year	1	20.2	18.73	<0.001
LogSR:year	1	19.4	3.88	0.063
Variance components		Component	Standard error	z.ratio
Compsition		0.1	0.04	2.788
Compsition:year		-0.1	0.02	-3.496
Residual		0.1	0.02	4.693

Table 4 Summary statistics from mixed-effects models for effects of crown proportional dissimilarity (PDS) on yearly litterfall overyielding in 2016.

	df	ddf	*F*	*P*
Intercept	1	25.1	35.52	<0.001
Site	1	25.2	0.59	0.45
PDS	1	24.7	3.28	0.08
Variance components		Component	Standard error	z.ratio
Compsition		0.49	0.42	1.18
Residual		1.53	0.42	3.65

Note: Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table. Abbreviations: ddf = denominator degree of freedom; logSR = $\log_2$(tree species richness). PDS = proportional dissimilarity of the vertical crown height; *F* and *P* indicate F-ratios and the P-values of the significance test.

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Chapter 4

Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest

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Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest

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Abstract

Aims
Litterfall, as an important link between aboveground and belowground processes, plays a key role in forest ecosystems. Here, we test for effects of tree species richness on litter production and litter quality in subtropical forest. The study further encompasses a factorial gradient of secondary succession that resulted from human exploitation. Given that a large percentage of subtropical forests are in secondary successional stages, understanding the role of biodiversity on forest re-growth after disturbance appears critical.

Methods
From January 2009 to December 2014, we monitored forest litterfall in 27 Comparative Study Plots that spanned a gradient of tree species richness (3–20 species) and secondary successional ages (~20 to 120 years) in Gutianshan Natural Nature Reserve, Zhejiang Province, China. The experiment is part of the biodiversity–ecosystem functioning research platform 'BEF-China'. Tree litterfall was collected in monthly intervals using litter traps. Samples were separated into leaf and non-leaf components. Leaf litter was further sorted into dominant and other species. Community level monthly leaf litter C and N contents were analysed through a full year. General linear mixed-effects models were applied to test for effects of tree species richness and successional age on litter quantity and leaf litter C/N.

Important Findings
Litterfall increased with species richness among and within successional age and this effect was consistent across years. Successionally older stands had higher litterfall and this effect was related to increased tree species richness. However, species richness did not change the intra- and inter-annual temporal stability of litterfall. Increasing tree species richness increased leaf litter quality (decreased C/N), while successional age had no effect. Our study indicates that more diverse forest stands produce more leaf litter and that this litter has higher N concentrations, which could promote forest growth through accelerated nutrient re-cycling.

Keywords: species richness, BEF-China, litterfall, leaf litter C/N, subtropical forest, secondary succession, structural equation models

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INTRODUCTION

Aboveground and belowground carbon dynamics are linked through litterfall, which thus is a key determinant of forest ecosystem functioning (Sayer and Tanner 2010). Positive effects of tree species richness on forest productivity have been found in several recent studies (Barufflo *et al.* 2013; Chen *et al.* 2016; Chisholm *et al.* 2013; LaManna *et al.* 2016; Morin *et al.*

2011; Zhang *et al.* 2012). However, diversity effects on litter production and litter quality have received less attention.

Previous studies have found a positive correlation between net primary productivity (NPP) and litterfall, with aboveground litter fluxes accounting for approximately one-third of NPP (Clark *et al.* 2001a; Gower *et al.* 1997; He *et al.* 2012; Malhi *et al.* 2011; Nouvellon *et al.* 2012). Increased productivity in more diverse forest (Baruffol *et al.* 2013) raises the possibility that litter production increases with species richness, which might lead to faster nutrient cycling. However, nutrient losses and re-cycling rates also depend on leaf litter quality (Li *et al.* 2017). One of the important indicators of leaf litter quality is its carbon to nitrogen ratio (C/N), which depends on leaf nutrient status and nutrient resorption and reflects the nutrient-use strategies of species and individuals (Vitousek 1984). At the community level, the quality of forest leaf litter will likely depend on the species composition of tree stands. Apart from that, leaf litter quality of the same species may also change with the diversity of the community in which trees grow.

Positive effects of tree species richness on litterfall have been found in a tropical forest biodiversity experiment (Scherer-Lorenzen *et al.* 2007), but only at low-diversity levels (three-species mixtures compared with monocultures), with no additional effect at higher species richness level (six-species mixtures). In the same study, effects on leaf litter C and N content were highly species–specific (Scherer-Lorenzen *et al.* 2007). A number of studies have compared litterfall in monocultures to litterfall in natural forests (e.g. Yang *et al.* 2004). However, natural forests generally have a more complex stand structure and differ in demographic dynamics, so that it is difficult to infer effects of tree species richness from a comparison with planted monocultures (Coursolle *et al.* 2012; He *et al.* 2012; Yang and Luo 2011).

With the rapid increase in human exploitation of natural resources, an increasing number of forests are in secondary successional stages. At later successional stages, tree growth slows down compared to younger stands (Chi *et al.* 2017). Older stands generally are characterized by a higher number of canopy species, fewer shade-tolerant species, higher standing biomass (Baruffol *et al.* 2013) and a higher investment into defense against herbivores and pathogens leading to lower leaf N content (Bruelheide *et al.* 2011; Kröber *et al.* 2012). For these reasons, effects of tree species richness on litterfall quality may depend on stand age.

To date, long-term investigations of the relationship between biodiversity and litterfall quantity and quality in natural forests with complex structure are scarce. It thus remains unclear how species richness contributes to the restoration of ecosystem processes and services through secondary forest succession. Such information is essential to understand forest restoration processes and to guide future reforestation. This is especially interesting in the face of climate change, supporting the northwards spread of subtropical plants in the northern hemisphere (Iverson *et al.* 2008).

Here, we measured tree litter production for six years in plots spanning largely independent gradients of tree species richness and forest successional age in species-rich subtropical forest. We hypothesized that (i) litterfall increases with species richness and that this effect increases with successional age; (ii) tree species richness decreases leaf litter C/N, i.e. improves leaf litter quality, and more strongly so in later successional stages.

MATERIALS AND METHODS

Study site

The present study was carried out in Gutianshan National Nature Reserve in the western part of Zhejiang Province, China (29°8′18″–29°17′29″N, 118°2′14″–118°11′12″E). This region has a typical subtropical monsoon climate with an annual average temperature of 15°C and annual average precipitation of *ca.* 2000 mm. The bedrock is comprised of granite and gneiss. Sandy–loamy and silty–loamy acidic Cambisols with pH ranging from 4 to 5 are the predominant soil type (Geißler *et al.* 2010).

Deforestation at the study site occurred during different periods since the 1950s, resulting in a patch structure with respect to successional age. Forest patches also vary in species richness, presumably due to variation in seed rain, natural recruitment and environmental conditions. In 2009, we established 27 plots with a size of 30 × 30 m each, called Comparative Study Plots. These plots span factorial gradients in tree diversity and successional ages (Bruelheide *et al.* 2011, see online supplementary Table S1). Stand age was defined as the age of the fifth-largest tree in a plot, with age determined from a stem core (Bruelheide *et al.* 2011). Because age is not a precise metric, we assigned plots to three age classes (young forest: 20–50; medium forest: 50–80; old forest: >80 years old).

In 2008, an inventory was conducted to assess tree species composition of each plot (Baruffol *et al.* 2013). Canopy trees, defined here by a diameter at breast height of at least 10 cm, comprised 1523 individuals belonging to 66 species, 49 genera and 29 families. In the present study, we use canopy tree species richness as metric of biodiversity for all analysis. The reason for this choice was that the litter traps we used were installed 1.5 m above ground and therefore mainly collected litter from canopy trees. Similar to successional age, plot-level tree species richness was categorized into three classes (low: 3–8, medium: 9–13, high: 14–20 species) to reflect the deliberate selection of plots belonging to these three richness categories.

Litterfall

In December 2008, four litter traps were set up in the corners of the central 10 × 10 m quadrat plus one in the middle of each plot. A nylon net (1 mm mesh) with a horizontal trapping area of 0.75 × 0.75 m was placed over a PVC frame 1.5 m above the ground.

Litterfall was collected monthly from January 2009 to December 2014. In December 2010 and July 2011, litter could not be collected because of heavy snow and rainstorm. Litterfall of these months was collected together with litter from the next month, and this amount was partitioned among the respective months based on the litter distribution in the other years. In 2010 and 2011, litter was first separated into leaf and non-leaf litter. The leaf litter was then sorted into the dominant species (*Castanopsis eyrei*, *Schima superba*, *Pinus massoniana*, *Cyclobalanopsis glauca*, *Quercus serrata* var. *brevipetiolata*, *Lithocarpus glaber*) and other evergreen and deciduous litter. The number of other evergreen and deciduous litter species per trap was also recorded from January to March of year 2010 and from April to December of year 2011. Non-leaf litter included fine branches (≤2.5 cm in diameter), bark, reproductive structures, animal detritus and other unidentified fine litter.

Litter was weighed after oven-drying at 80°C for 24 h. Leaf litter samples of the year 2010 were pooled by plot, ground using a ball mill (NM200, Retsch, Haan, Germany) and C and N concentrations determined by dry combustion (2400 II CHN elemental analyzer, Perkin-Elmer, USA).

Statistical analyses

The effects of year (1–6), month (1–12), successional age (1–3), species richness (3–20) and their interactions on litterfall and leaf litter quality were analyzed with linear mixed-effects models using ASReml-R (Butler *et al.* 2007). All fixed-effects terms in the model were fitted sequentially. Litterfall amounts were square root-transformed prior to analysis to meet the requirements of normal distribution and homoscedasticity of residuals.

For yearly litterfall data, the fixed-effects terms were fitted in this sequence: YEAR + div + lin(age) + AGE + YEAR × div + YEAR × lin(age) + YEAR × AGE + div × lin(age) + div × AGE. The random-effects terms used were plot, modeling the random sampling of plots, and the interaction plot × YEAR, which corresponded to the residual. Interactions are denoted by a × operator. Capitalized terms YEAR (6 levels) and AGE (3 levels) are factors, while lin(age) is a continuous integer variable, i.e. the linear contrast of factor AGE. Similarly, div is a continuous integer variable and stands for species richness.

Monthly litterfall data were analyzed with a mixed-effects model with plot, plot × MONTH and plot × YEAR as random effects and factor MONTH (12 levels), species richness, successional age and their interactions as fixed terms. Leaf C/N was analyzed similarly excluding terms containing YEAR.

Because plot species richness was positively correlated with successional age ($r = 0.64$, $P < 0.01$), we reversed the order of tree species richness and successional age to investigate the degree of confounding of effects (Baruffol *et al.* 2013; Schmid *et al.* 2017). Species richness effects fitted before successional age indicated the overall species richness effect, whereas richness fitted after successional age indicated effects of species richness after adjusting for successional age (i.e. effects of species richness within successional age).

RESULTS

Environmental effects

Site conditions (see online supplementary Table S1), including elevation, slope, aspect, slope inclination, soil pH, soil moisture and soil total C and N content did not correlate significantly with tree litterfall or leaf litter C/N (Pearson's product moment correlations, $P > 0.05$).

Litterfall quantity

Annual litterfall varied among years and plots, ranging from 2.6 Mg ha^{-1} year^{-1} to 7.9 Mg ha^{-1} year^{-1}, with a mean value of 5.4 Mg ha^{-1} year^{-1}.

Canopy tree species richness significantly positively affected yearly total litterfall [Fig. 1a, Table 1a, $P < 0.001$ in mixed-effects model when div was fitted before lin(age) and AGE; $P < 0.05$ when div was fitted after lin(age) and AGE]. The positive effect of species richness was also observed in a structural equation model (see online supplementary Fig. S1). The positive effect of species richness was similar at different successional ages [Fig. 1a, Table 1a, $P = 0.64$ for div × lin(age)]. Species richness effects were independent of year (Table 1a, $P > 0.05$ for YEAR × div).

Yearly litterfall increased with forest stand age if influences of species richness were ignored [Fig. 1a, Table 1a, $P < 0.01$ for lin(age) fitted before div]. However, the main effect of

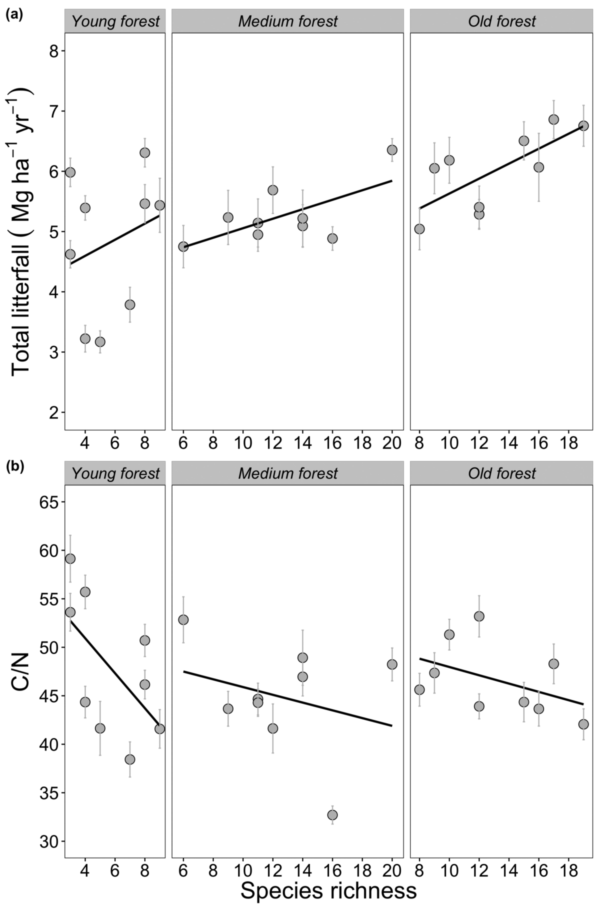

Figure 1: (a) total litterfall per year and (b) leaf litter C/N (mass ratio) as functions of species richness in different successional ages. Error bars indicate means ± standard errors ($n = 6$ for total litterfall, $n = 12$ for C/N).

Table 1: results of three alternative sequential mixed-effects models for yearly, monthly litter production and leaf litter C/N

(a) Yearly litterfall data from 2009 to 2014					
Model 1			Model 2		
Fixed terms	*F* value		Fixed terms	*F* value	
YEAR	$F(5,115) = 26.51$	***	YEAR	$F(5,115) = 26.51$	***
div	$F(1,21) = 11.47$	**	lin(age)	$F(1,21) = 9.82$	**
lin(age)	$F(1,21) = 1.55$	n.s.	AGE	$F(1,21) = 0.12$	n.s.
AGE	$F(1,21) = 1.42$	n.s.	div	$F(1,21) = 4.50$	*
YEAR × div	$F(5,115) = 2.14$	.	YEAR × lin(age)	$F(5,115) = 3.71$	**
YEAR × lin(age)	$F(5,115) = 2.26$	.	YEAR × AGE	$F(5,115) = 2.63$	*
YEAR × AGE	$F(5,115) = 3.61$	**	YEAR × div	$F(5,115) = 1.67$	n.s.
div × lin(age)	$F(1,21) = 0.00$	n.s.	lin(age) × div	$F(1,21) = 0.00$	n.s.
div × AGE	$F(1,21) = 0.23$	n.s.	AGE × div	$F(1,21) = 0.23$	n.s
Random terms	Variance component		Standard error of variance component		
Plot	3.0437			1.0179	
Residuals	1.5172			0.2001	
(b) Monthly litterfall data from 2009 to 2014					
MONTH	$F(11,253) = 81.68$	***	MONTH	$F(11,253) = 81.68$	***
div	$F(1,21) = 9.91$	**	lin(age)	$F(1,21) = 7.73$	*
lin(age)	$F(1,21) = 0.97$	n.s.	AGE	$F(1,21) = 0.02$	n.s.
AGE	$F(1,21) = 0.96$	n.s.	div	$F(1,21) = 4.08$	.
MONTH × div	$F(11,253) = 1.88$	*	MONTH × lin(age)	$F(11,253) = 1.84$	*
MONTH × lin(age)	$F(11,253) = 1.26$	n.s.	MONTH × AGE	$F(11,253) = 0.51$	n.s.
MONTH × AGE	$F(11,254) = 1.07$	n.s.	MONTH × div	$F(11,253) = 1.86$	*
div × lin(age)	$F(1,21) = 0.00$	n.s.	lin(age) × div	$F(1,21) = 0.00$	n.s.
div × AGE	$F(1,21) = 0.73$	n.s.	AGE × div	$F(1,21) = 0.73$	n.s.
Random terms	Variance component		Standard error of variance component		
Plot	0.2071			0.0905	
Plot × YEAR	0.2526			0.0359	
Plot × MONTH	0.4306			0.0459	
Residuals	2.5165			0.0372	
(c) Monthly leaf litter C/N data of year 2010					
MONTH	$F(11,249) = 13.69$	***	MONTH	$F(11,249) = 13.69$	***
log(div)	$F(1,21) = 6.52$	*	lin(age)	$F(1,21) = 0.26$	n.s.
lin(age)	$F(1,21) = 2.76$	n.s.	AGE	$F(1,21) = 1.37$	n.s.
AGE	$F(1,21) = 0.071$	n.s.	log(div)	$F(1,21) = 7.72$	*
MONTH × log(div)	$F(11,248) = 0.51$	n.s.	MONTH × lin(age)	$F(11,248) = 0.62$	n.s.
MONTH × lin(age)	$F(11,249) = 0.88$	n.s.	MONTH × AGE	$F(11,250) = 0.81$	n.s.
MONTH × AGE	$F(11,250) = 0.89$	n.s.	MONTH × log(div)	$F(11,249) = 0.84$	n.s.
log(div) × lin(age)	$F(1,21) = 0.78$	n.s.	lin(age) × log(div)	$F(1,21) = 0.78$	n.s.
log(div) × AGE	$F(1,21) = 0.06$	n.s.	AGE × log(div)	$F(1,21) = 0.06$	n.s.
Random terms	Variance component		Standard error of variance component		
Plot	23.83			8.137	
Plot × MONTH	21.44			2.707	
Residuals	41.93			1.671	

F values and corresponding degrees of freedom (numerator and denominator d.f.; in parentheses) are given. YEAR (6 levels), AGE (3 levels), MONTH (12 levels) are fixed-effects factors, while div, log(div) and lin(age) are continuous integer variables, i.e. lin(age) is the linear contrast of the factor AGE. The fixed-effect term div stands for canopy tree species richness, log(div) for the logarithm of div. Significance levels: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, $\cdot P < 0.1$, not significant: n.s.

successional age became statistically insignificant when it was adjusted for species richness [Table 1a, $P > 0.1$ for lin(age) fitted after div]. The notion that age effects might have been mediated by species richness changes was supported by structural equation modelling (see online supplementary Fig. S1, no significant direct path from successional age to litterfall). Litterfall gradually increased with year [Fig. 2, anova with lin(year) as continuous variable, $F_{1,134} = 18.27$, $P < 0.01$], and this effect was more pronounced in medium age or old forest (Fig. 2).

The analysis of monthly litterfall data revealed a dependence of species richness effects on season (Table 1b, $P < 0.01$ for MONTH × div; Fig. 3). Different litterfall components had different monthly dynamics (Fig. 3). Leaf litterfall showed a bimodal temporal trend, whereas non-leaf litterfall did not. Positive species richness effects were found for total and leaf litterfall only in months with high litter production (April–May, October–November; Fig. 3a and b).

Neither the intra-annual (seasonal) nor the inter-annual stability of litterfall production depended on species richness (Fig. 3, see online supplementary Fig. S2).

Litter species composition

Higher species numbers were found in the traps in more species-rich plots, especially in months with high litterfall (Fig. 5). As for litterfall, litter species richness followed a bimodal temporal pattern for evergreen species, but a unimodal pattern for deciduous species (Fig. 5). In general, litterfall from the highly productive dominant species *Schima superba* and *Castanopsis eyrei*, as well as other evergreen and other deciduous species, was higher in species-rich plots and in later successional stages (Fig. 6).

Leaf litter C/N

Leaf litter C/N, a proxy for litter quality, averaged 46.4 ± 1.1 g C (g N)$^{-1}$ (50.2 ± 14% C; 1.1 ± 3% N). Total leaf litter C return

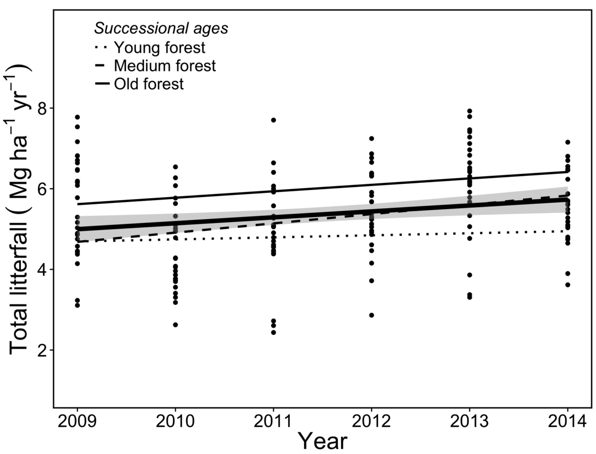

Figure 2: total litterfall per year in different successional ages (see legend inside figure). Thick solid line indicates the linear regression line based on the grand mean of each plot (n = 27). The grey shadow shows the 95% confidence interval.

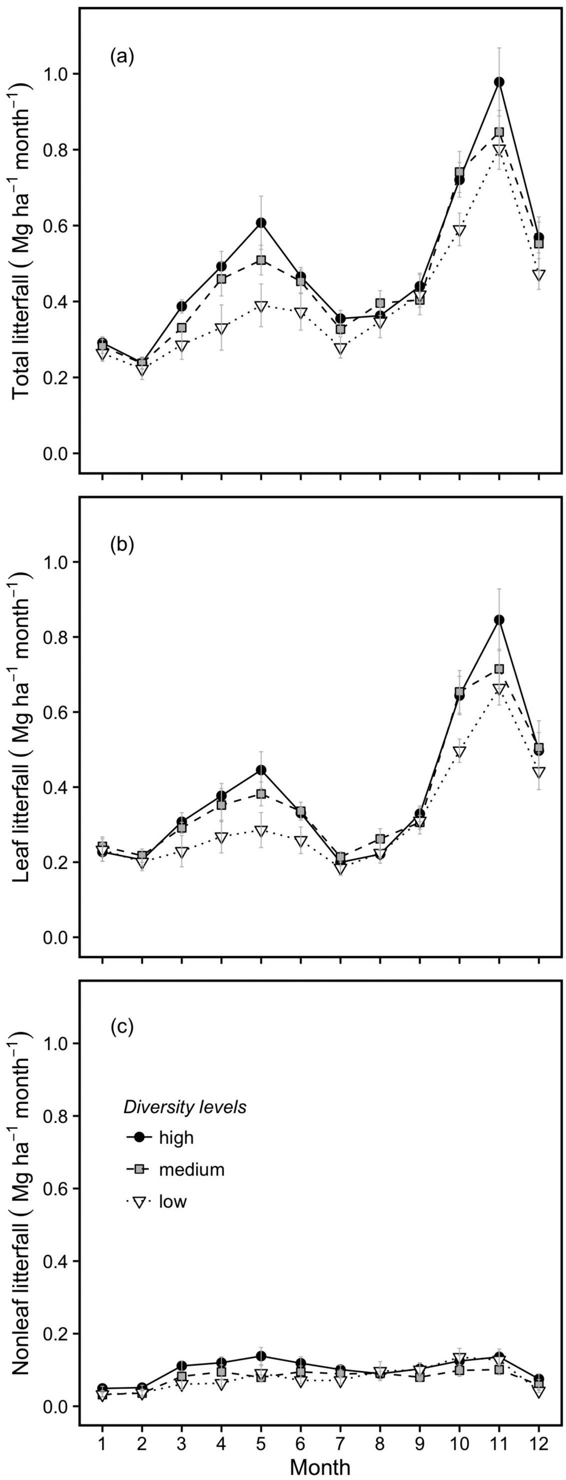

Figure 3: (a) total monthly litter production, (b) monthly leaf litter production and (c) monthly non-leaf litter production at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

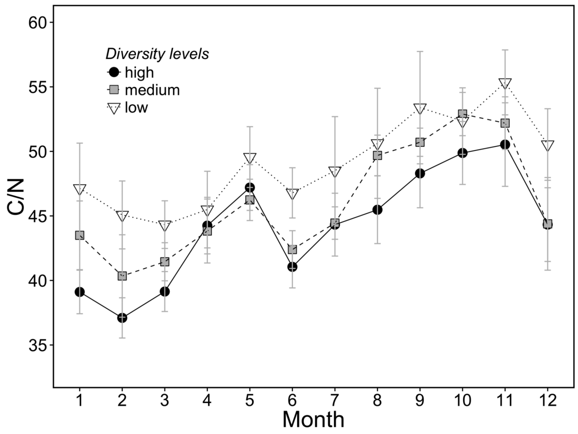

Figure 4: monthly leaf C/N (mass ratio) at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

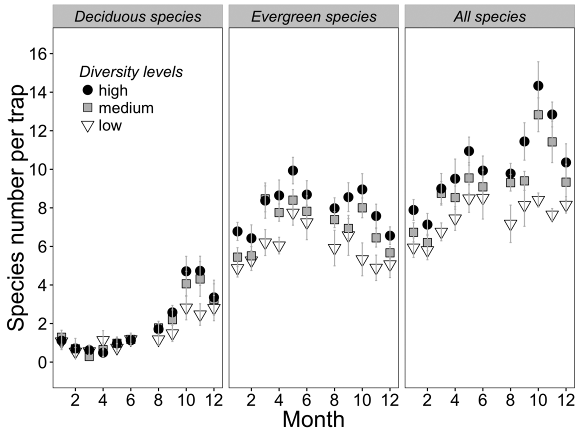

Figure 5: monthly litter species number per trap at different species richness levels for deciduous and evergreen species and for all species combined. Error bars indicate means ± standard errors (n = 9). Circles refer to high-, squares to medium- and triangles to low-diversity plots.

was 1720 ± 123 kg C ha^{-1} year^{-1} and N return 38.6 ± 2.8 kg N ha^{-1} year^{-1}. Leaf litter C/N decreased significantly with increasing tree species richness [Figs. 1b and 4, Table 1c, $P < 0.05$ with div fitted before lin(age) and AGE; $P < 0.05$ with div fitted after lin(age) and AGE]. Leaf C/N did not depend on successional age [Fig. 1b, Table 1c, $P > 0.05$ for lin(age) and AGE fitted before or after log(div)].

DISCUSSION

Our results showed a strong positive effect of species richness on both litterfall amounts and leaf litter quality (Tables 1a and b). This finding parallels strong positive, density-mediated tree

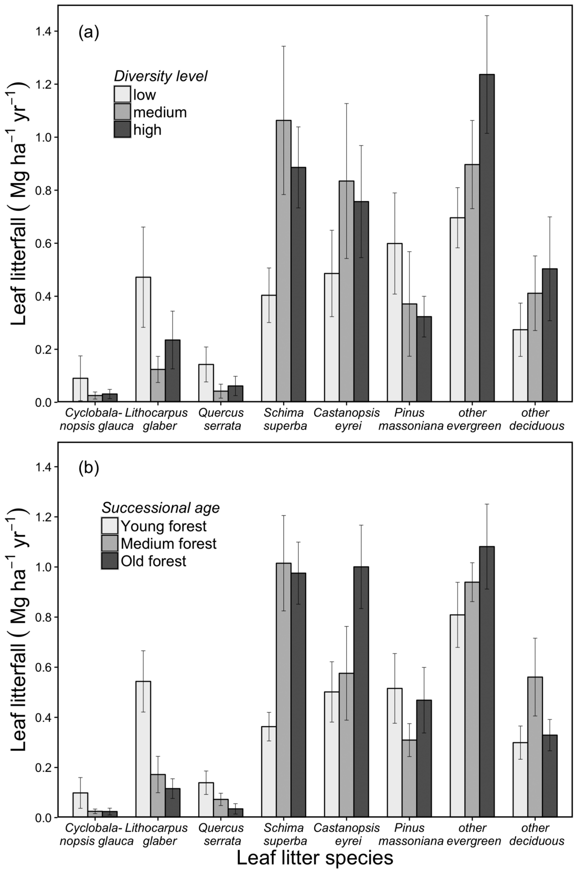

Figure 6: production of different species' leaf litter at (a) different species richness levels and (b) along different successional stages (see legends inside figure). Error bars indicate means ± standard errors (n = 9).

diversity effects on stand total basal area and growth in the same plots (Baruffol *et al.* 2013). Baruffol *et al.* (2013) argued that the larger number of tree individuals found in more diverse plots possibly resulted from complementarity among species, i.e. that more complementarity among species reduced competition among heterospecific trees and allowed for denser stands at higher species richness. Belowground benefits from complementarity may also have contributed to higher total leaf production (Bessler *et al.* 2009; Bu *et al.* 2017; Sun *et al.* 2017). Interestingly, positive effects of species richness on leaf area were also found in a designed experiment with constant tree density (Peng *et al.* 2017). The increase in litterfall with diversity may thus also have been caused by higher leaf production of individual trees in more diverse forest stands (Clark *et al.*, 2001a). Overall, this suggests that more diverse forest stands produce more leaf litter, and that this effect can but must not necessarily be mediated by an increased density of tree individuals alone, but also by increasing leaf production.

The higher leaf litter nitrogen contents in more diverse plots may indicate an improved supply of trees with nitrogen and/or a lower nutrient resorption efficiency. In forests, nutrient concentrations of newly fallen leaf litter often correlate positively with nutrient concentrations of fresh leaves (Aponte *et al.* 2013). An additional possible explanation for the observed effects in our study is that deciduous broad-leaf tree litter production increased with species richness (Fig. 6a). These species generally have higher green fresh leaf N concentrations than evergreen or conifer species (Han *et al.* 2005; Kröber *et al.* 2012; McGroddy *et al.* 2004). It is conceivable that this change in species composition with increasing species richness was part of the mechanism underlying the positive species richness effects on litterfall N fluxes. Because the quality of litterfall is a major controller of litter decomposition and nutrient return rates (Manzoni *et al.* 2008; Meier and Bowman 2008), the lower initial litter C/N ratio in more species-rich plots in our study could accelerate decomposition and nitrogen mineralization. Tree species diversity might thus promote productivity by increasing nutrient availability.

The species richness effects we found were independent of successional age. Our hypothesis of a stronger biodiversity effect in later successional stages was rejected. This suggests that even in young forests tree species diversity already plays an important role. Higher litterfall in old successional forests has been attributed to larger standing leaf canopies as well as to decreased physiological function of older trees (Drake *et al.* 2011). Our analysis suggests that increased species richness may be a further factor increasing litterfall in older secondary forests, which is consistent with the effects on woody growth pattern (Baruffol *et al.* 2013; see online supplementary Fig. S1, Tables 1a and b).

Our findings contrast with those of other studies in which no significant effects of tree diversity on litter production and litter N content were found (Scherer-Lorenzen *et al.* 2007). However, in those previous studies, lower diversity levels were compared (species richness levels 1, 3, 6) whereas in our study the range of species richness values was considerably larger (3–20 species).

In our study we did not find a significant effect of successional age on the leaf litter C/N (Table 1c). This does not support the assumption that there should be a change in resource-use strategy from high nutrient acquisition to nutrient retention with succession. It also does not support the assumption that trees should increasingly allocate more energy to defense which may decrease leaf litter quality (Kröber *et al.* 2012). However, regarding the first assumption, nutrient resorption efficiency may also be higher in earlier successional stages, serving the higher demand for nutrients in faster-growing trees (Yuan and Chen 2010). Regarding the second assumption, former research in the same study plots has shown that while green leaf physical resistance increased, chemical defense traits, such as tannin and phenolics concentrations, decreased with forest successional age, such that the litter decomposition rates remained stable along secondary succession (Eichenberg *et al.* 2014). Positive and negative effects may have acted together and thus caused leaf litter C/N to remain stable with successional age.

In conclusion, tree species diversity rather than forest successional age seemed to play the major role in affecting leaf litter quantity and quality. More litter production and better leaf litter quality in more diverse forest stands could promote higher soil microbial and fauna diversity and create more favorable conditions for decomposition and nutrient release, thus stimulating increased tree growth.

SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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Discussion

Discussion

This study provides the first comprehensive experimental evidence and explanations for positive biodiversity effects on forest productivity and carbon accumulation using a large number of replicates, realistic tree densities and large plot sizes across a wide range of species richness levels.

Positive diversity effects increase with time

With the use of the additive partitioning method, I found positive complementarity effects and small negative selection effects in the experiment. This is consistent with results from studies in the Sardinilla project in Panama, where significant complementarity effects combined with small, non-significant selection effects were found in a study of aboveground nutrient pools (Zeugin *et al.* 2010). However, the present study is the first in forest experiments to report an increasing biodiversity effect in forests over time and this is due to increasing complementarity. This is an important finding that has previously only been known from grassland experiments (Reich *et al.* 2012). In their study, authors pointed out that this insight is critical to understand how the shape of the BEF relationship changes with time, because it indicates the extent to which even a slight decrease in species richness will influence biomass production. They found highly diverse species combinations that showed a high degree of functional redundancy during early years became more functionally unique through time. In grasslands, species are typically short-lived and community selection may happen quickly. Communities become increasingly different in their leaf functional traits in higher diversity plots through the selection for individuals with greater niche differentiation among species in plant mixtures (Zuppinger-Dingley *et al.* 2016). In addition, a more pronounced negative plant-soil feedback was reported for monocultures (Zuppinger-Dingley *et al.* 2014). However, in forests trees feature large and long-lasting vertical structures which allow them to continuously accumulate biomass over time. Thus the mechanisms differ from those in grasslands.

Niche complementarity effects based on light use

In Chapter 1, we found that vertical crown complementarity increased selection effects, probably due to an asymmetric competition for light. In addition to relations in the often-studied trait space, niche axes can also include physical space. Sapijanskas *et al.* (2014) showed that tree diversity enhanced community-level light capture through enhanced tree growth and suggested at least three size-independent mechanisms: architectural differences, temporal niche differences, and morphological plasticity. Our study may be interpreted in the light of these mechanisms, and also further implied that physical space niches can change across time. Light harvesting reaches higher efficiency in tightly packed tree crowns in diverse forests. This packaging may vary in its vertical spatial distribution over time and the temporal packaging may differ among species, thus allowing for dynamically filling niches in space and time.

Enemy-based niche complementarity effects

In forest ecosystems, intense multi-trophic interactions (e.g. between plants and herbivores) take place aboveground. This thesis presents insights in the mechanisms that act across trophic levels, enlarging the BEF concept to multi-trophic interactions within forests. I found that the reduction of leaf pathogen-mediated damage through the application of a fungicide dampened the positive biodiversity–productivity relationship. A more diverse forest community could hinder pathogen transmission and thus decrease overall leaf pathogen damage, which is an essential mechanism for the positive effects of tree species richness on productivity. I further found that fast-growing trees benefit most from a decrease in leaf pathogen-load, because they produce leaves of higher substrate quality and are more susceptible to infestation. However, the story is different with leaf herbivory by insects, which increases with tree diversity and can move across plots much easily (Schuldt et al. 2017). The reduction of insect herbivore pressure through the application of an insecticide had no significant effects on the relationships between tree species richness and productivity.

Other positive species interactions, i.e. facilitation

I further studied tree species richness effects on forest litter production, an important ecosystem function to link the above- and belowground processes. I showed that tree species richness also increased litter production and leads to community leaf litter mixtures that are of higher nutritional quality. Other research in BEF-China has demonstrated that tree diversity positively affects mineralization rates (Trogisch *et al.* 2016) and a study by Pei *et al.* (2017) gave evidence for a positive relationship between litter species diversity and abundances of mycorrhizal fungi as well as actinomycetes. Thus, higher leaf litter production in diverse communities may imply a faster nutrient cycling. Increased mineralization rates due to higher inputs of leaf litter through diverse tree communities could help to increase overall forest stand performance, which may be an important mechanism for positive forest BEF relationships (Sapijanskas *et al.* 2013). Increasing positive interactions between tree species (e.g. facilitation by neighbors with increasing litter input) may also affect or even cause the increasing positive diversity effect over time.

Linking results from manipulated experiment to real natural forest

This thesis also covers further novel findings related to additional shrub-diversity, plot-size treatments, as well as economic tree species plantation plots. Such treatments are relevant for the transfer of the mechanistic understanding gathered in experiments to natural situations, but they have never been tested before. By setting up a similar kind of litter experiment in comparative study plots with different diversity levels in nearby natural forest, the same relationships between species richness and litterfall as in the manipulative field experiment were found. These findings are in contradiction to what has been reported from a comparison between experimental plots and a natural forest ecosystem in Panama (Ruiz-Jaen & Potvin 2011). The authors reported different patterns of relations between species diversity and forest carbon stocks in natural forests compared with mixed-species plantations. In contrast to the study of Ruiz-Jaen & Potvin, the experimental plots of the BEF-China project were established on sites featuring a natural and highly heterogeneous topography with big plot sizes (666.7 m^2 for each plot). Strikingly we found that the results from our experimental setup were similar to the findings in natural forests. It turned out that the tree species richness effects were all positive and they all followed a similar pattern. Thus, it is possible that we can interpret forest BEF processes and mechanisms in natural forests as comparable to those from manipulative field experiments, given the topographic features of the two systems are comparable.

Carbon fixation to mitigate climate change

In this thesis, I showed that strong biodiversity effects rapidly develop even in young forests as early as three to seven years after initial establishment. These positive biodiversity effects lead to a much higher carbon accumulation in species-rich than in species-poor forest stands. Indeed, after seven years the most diverse stands already stored as much carbon as the most productive plantation species typically used in huge afforestation projects in China. Another important facet of BEF relationships that is, however, not covered in the present thesis is known as the insurance hypothesis (Loreau *et al.* 2003; Tilman *et al.* 2006). This hypothesis states that biodiversity can enhance the overall stability of a community. A hint for the existence of such an insurance effect of tree diversity in forest restoration has been reported from another forest biodiversity experiment in Sabah, Borneo (Tuck *et al.* 2016). Thus it suggests that a change in re- or afforestation policies from monocultures to diverse forests would not compromise productivity and carbon storage but yet contribute to the maintenance of biodiversity and at the same time allow for a sustainable biomass production and carbon fixation.

Transfer knowledge to forest management

This thesis shows important findings regarding the role of biodiversity on forest productivity, a fact that most non-academic stakeholders are not aware of. Our results can be directly linked to ongoing assessments aimed for political consulting. Here, our results may be used to strengthen the bands in the science–policy interface as we give strong arguments for the maintenance of biodiversity and its role in the sustainable provision of important ecosystem services. During my PhD, I promoted the knowledge transfer between scientists and different stakeholders (Fig. 1, Appendix 3). To identify the key services that are recognized and valued by society, I carried out interviews with local farmers, forest managers, students, teachers and other residents in five villages near the field experiment (Appendix 1, 2). This study allowed for the identification of those indicators that are most meaningful to the different stakeholders. With this I obtained a sound understanding of their attitudes towards forest diversity (Appendix 1). Our experimental design and monitoring for ecosystem services to support decision-making was greatly enhanced by the early involvement of stakeholders involved in forest management. We realized that local people lack the awareness for the significance of biodiversity. They like planting trees in monocultures (mainly Chinese fir, a species also included in our experiment). As the forest policy in China is becoming increasingly strict now, this results in less deforestation and more afforestation. Especially here, more scientific consulting to provide guidance for afforestation is of great benefit to local people and is urgently needed.

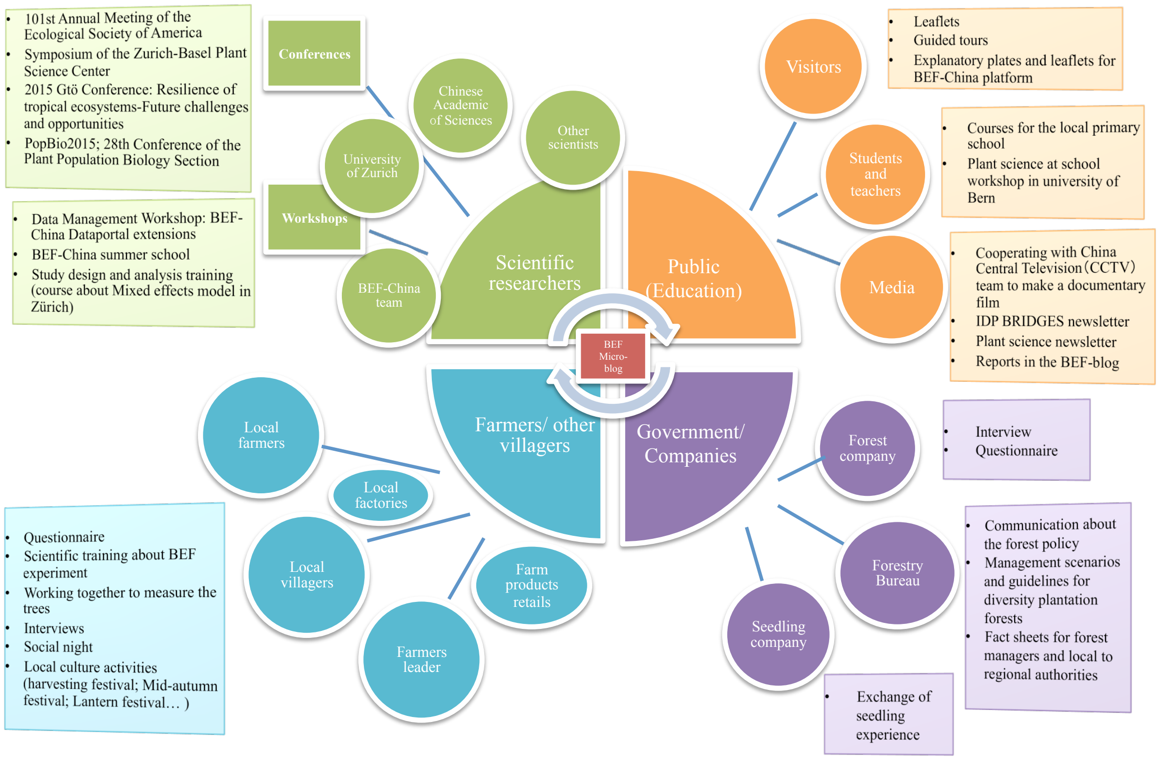

Fig. 1 Stakeholders map. Circles represent related stakeholders, while squares represent related activities.

Future research

The present thesis focused on the results determined in studies from one out of several extinction scenarios established in the BEF-China platform: the random species extinction scenario. In order to reflect consequence of more realistic species extinctions and to get the effect of species loss, it is necessary to also assess BEF relationship from non-random extinction scenarios, which are assumed to be a more realistic model of species decline in natural forest ecosystems. Trees in forests are long lived and occupy large vertical space.

Thus long-term data from manipulated field experiment as well as from natural forests are important. Another promising future focus could lie on the interaction among the herb layer, shrub and tree layer.

More analysis tools and methods need to be created to allow deeper insights into the relationships between biodiversity and ecosystem functioning. In manipulated experiments, the additive partitioning method derived from the Price equation allows to decompose diversity effect in complementarity effect (CE) and selection effect (SE). Yet, intra-species interactions and the neighborhood plasticity have never been considered with this method. These additional facets may also differ among diversity levels. Even if there are no inter-species interactions, species may perform differently in more diverse communities. A great advantage when doing research in forests compared with grasslands is that single individuals may be easily identified and separated. Thus, individual based analyses to test inter- and intra-species interactions and link them to overall community performance will be important. Furthermore, the dilution effect caused by decreasing species abundance instead of species interactions (e.g. facilitations, competitions, etc.) may be difficult to separate from CE. Another issue of addition partition method is CE and SE are necessarily correlated, since net effect is, by definition, the sum of CE and SE. Thus new methods are needed to conquer these issues.

In the observational studies there are new tools to separate the species richness, composition and abundance effects from other environmental variations. However, these tools have a certain set of (sometimes very strong) *a-priori* assumptions that can't be controlled. Therefore such models can't be easily applied in order to elucidate underlying mechanisms. To allow for a better comparison between manipulated field experiments and real natural ecosystems, the development of powerful statistical tools (e.g. Bayesian modeling, applying Price equation to partition variations) to isolate diversity effects from other confounding factors in observational or comparative studies may be necessary. Structural equation modeling (SEM) may be a useful tool to convincingly demonstrate causal effects of ecosystem properties on diversity or the other way around. This might help to separate biodiversity effects caused by community assembly from effects of environmental factors on species coexistence. In manipulated experiments, it will be of great importance to assess the relative importance of the effects of genetic diversity, functional diversity, species identity and species interaction effects within the overall species richness effects.

Even more interestingly, BEF relationships in the context of different trophic levels (Soliveres *et al.* 2016) and different environmental conditions in different scales are worth to be explored in more detail. Currently there are many networks, such as the TreeDivNet, and it is highly interesting to compare those manipulated experiments with diversity relations obtained from natural ecosystems. Here, comparing the patterns and mechanisms explored in small plots and scale them up to regional scales will be very important. In addition to productivity alone, additional ecosystem functions should be taken into account to get a measure of ecosystem multifunctionarity (Allan *et al.* 2015) in forests. Considering different ecosystem functions across different trophic layers should be the focus of a more advanced BEF research in the future.

In summary, this thesis presents evidence for strong positive biodiversity effects on forest productivity in a subtropical manipulative field experiment which increased with time. Several new mechanisms are discovered and discussed. Despite continued forest conversion and degradation, forest cover is increasing in some countries across the globe, particularly in China. However, new forests plantations for commercial and restoration purposes are mostly established as monocultures. This thesis demonstrates that plantations with diverse species can improve ecosystem services, especially carbon storage. Thus, planting diverse forest plantations offers a win-win solution in terms of mitigation of climate change as well as contributing to biodiversity maintenance and sustainability.

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RESEARCH EXPERIENCE

09/2013–current Biodiversity and Ecosystem Functioning Project:
The role of tree and shrub diversity for production, erosion control, element cycling, and species conservation in Chinese subtropical forest ecosystems (BEF-China)

1/2010–07/2013 Biodiversity and Climate Change, A Risk Analysis:
Risk analysis of biodiversity change: a case study in a subtropical forest, China

07/2011 Sino-Swiss Summer School at the Alpine Biology Center, Ticino, Switzerland:
Effects of bedrock on plant community structure in the Swiss Alps

07/2010 Sino-Swiss Summer School in Haibei, Qinghai, China:
Effects of fertilization on arbuscular mycorrhizal colonization of high-altitude grassland plants

07–08/2008 National Ministry of Science and Technology Platform Project:
Plant specimens' digitalization, integration and sharing platform construction in Gutianshan National Nature Reserve

WORKSHOPS/TRAINING

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06/2016 iDiv Summer School — Biodiversity Synthesis and Integration; Leipzig, Germany:
Make it spatial — Simulating scale-dependent causes and consequence of coexistence mechanisms

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07/2014	Ecology of Alpine Plants; Furka Pass, 2450 m, Switzerland: Micro-topography affects small scale plant species composition and diversity in alpine zone

TEACHING EXPERIENCE

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2014–2015	Introduction to Statistics
2016	Behavioral Biology
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PRESENTATIONS

05/2017	PopBio2017 – 30th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ); Halle (Saale), Germany: Poster “Biodiversity increases wood production in a forest experiment”
08/2016	101st Annual Meeting of the Ecological Society of America 2016 (ESA); Fort Lauderdale, Florida, USA: Talk “Leaf pathogens and herbivores drive plant diversity–productivity relationships in a subtropical forest experiment”
05/2016	Plant science at school; Institute of Plant Sciences, Bern: Invited talk “Diversity and productivity in subtropical forests — fixing carbon to mitigate climate change”
04/2015	GfÖ conference: Resilience of tropical ecosystems — Future challenges and opportunities; Zurich, Switzerland Talk “Resources and enemies, which have bigger influence on the biodiversity–ecosystem functioning relationship in the subtropical forest?”
12/2015	Symposium of the Zurich-Basel Plant Science Center “Unlocking the Potential of Diversity”; Zurich, Switzerland: Poster “Resources and enemies, which have bigger influence on the biodiversity–ecosystem functioning relationship in subtropical forest?”
05/2015	28th Conference of the Plant Population Biology Section (PopBio); Tübingen, Germany: Poster “Spacial and temporal effects on the relationship between species diversity and aboveground primary productivity in subtropical forest”

PUBLICATIONS +equal contribution

9) **Huang,Y**., Chen, Y., ..., Ma, K., Niklaus. A. P., Schmid, B. Causes of strong positive biodiversity–productivity relationships in a large-scale subtropical forest biodiversity experiment. *In preparation*

8) **Huang,Y**., Ma, K., Niklaus. A. P., Schmid, B. Do negative density-dependent effects of consumers and pathogens drive plant diversity–productivity relationships in subtropical forest? An experimental test in a large-scale afforestation. *In preparation*

7) **Huang, Y.,** Ma, Y., Zhao, K., Niklaus, P.A., Schmid, B. & He, J.-S. (2017) Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest. Journal of Plant Ecology, 10, 28-35.

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2) Ma, Y., Geng, Y., **Huang, Y**., Shi, Y., Niklaus, P.A., Schmid, B. & He, J.-S. (2013) Effect of clear-cutting silviculture on soil respiration in a subtropical forest of China. Journal of Plant Ecology, 6, 335-348.

1) **Huang Y.,** Olbrecht L., Yang X., He J.-S. (2013) Effects of nutrient additions on the colonization of arbuscular mycorrhizal fungi in the alpine meadow on the Tibetan Plateau. Acta Scientiarum Naturalium Universitatis Pekinensis, 50, 911-918 (in Chinese).

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Appendix

Appendix 1

Local people's awareness and attitudes towards forest diversity and ecosystem services

A questionnaire survey was carried out in seven villages in Jiudu town, Jiangxi province, China. The seven villages are Qiankeng, Shijia, Xinjian, Dongde, Xingangshan, Jiudu and Tiquan, all located around the BEF-China experiment (Fig. 1). At least 20 people from each village were interviewed to answer questions on a standard questionnaire (Appendix 2) that was designed to assess the subjects' awareness and attitude toward forest biodiversity and ecosystem services. In order to find out people's attitude towards forest diversity, pictures of mixed forests vs. monocultures were handed out and people were asked to the picture regarding to the questions. In total, 150 full questionnaires were collected, comprising answers from 62 female and 88 male subjects. I divided different professions of subjects into three categories — Farmers (including all farmers and housewifes); Workers (including workers, people who had their own individual business); White-collar (including student and people who worked in the government or institutions).

The results showed that 91 persons (60.7%) haven't ever heard about biodiversity, but 83.3% people think that experts are needed to maintain and protect forests (Fig. 2). A higher proportion of people think mixed forests are more interesting, less boring, less disturbed and contain more diverse communities of plants and animals (Fig. 3b, e, f, g, h). However, more people like monocultures over mixed forest stands, possibly because they think monoculture forests are more familiar and more comfortable to enter (Fig. 3 a, c, i). Interestingly, ordination methods (Fig. 4) showed that people who experienced higher levels of education or whose profession is more directed towards mental work, tended to prefer mixed forests. The ordination clearly shows a segregation of two gradients in the two dimensional space: the first ordination axis (21.6% of explained variance) represents a gradient from interest in forest monocultures on the left side to higher interest in mixed forests on the right side. Along this axis a clear segregation was observed between a preference for monocultures (likemono) in people working in direct dependency to forest ecosystems (farmers) to a preference for forest mixtures (likemix) in people whose labor is less directly related to forest ecosystems (workers and white-collar, Fig. 4a). The same holds if the subjects were categorized according to their levels of education: people with no education whatsoever were more attached to monocultures whereas subjects that had undergone higher levels of education were more attached to forest mixtures (Fig 4b). The second ordination axis (11.5% of explained variance) represents a gradient that is reflecting the opinion towards habitat provisioning of forests: on the lower end subjects are located with the believe that monocultures host higher numbers of plant species (plantmono), whereas in the upper end, subjects responded that they believe mixtures host higher numbers of plant species (plantmix). Interestingly, the ordination reveals that those people who believe that monocultures host a higher number of plant species are less familiar with mixed forests (negative correlation between plantmono and familiarmix in Fig. 4), whereas the opposite relation was found for those who believe that forest mixtures hold higher numbers of plant species (negative correlation between plantmix and familiarmono in Fig. 4).

I also did a survey on people's opinion on the importance of different ecosystem services. Ecosystem services were categorized into Cultural services, Provisioning services, Regulating services and Supporting services. While people generally valued the Cultural services of forest ecosystems (with the exception spiritual/religious values), it turned out that Provisioning services, especially providing fuel, is of comparatively low importance for local people (Fig. 5). However, within the category of Provisioning services, the use as a source for timber is of high importance to the local population. Interestingly, most people value Regulating services. They perceive forests as an important to protection against natural hazards (e.g. erosion), and acknowledge its importance in the production of clean air and water, as well as in climate regulation (Fig. 5).

With the ordination method, Fig. 6 shows that there is a clear gradient on the first axis (27.2 % of explained variance) between cultural and provisioning services. Here, people whose work is more related to mental work (Fig. 6a) or that experienced a higher level of education (Fig. 6b) show a higher valuation for the non-existential (i.e. not necessary to survive) services. The pattern is more pronounced when considering peoples educational levels as depicted in Fig. 6b. However, the basic tendency is the same as when a subject's labor class was used for the assessment. The second axis (20% of explained variance) segregates Provisioning services from the Supporting services. Here, farmers (Fig. 6a) or people with lower levels of education (Fig. 6b) tend to value regulating services more than people from the white-collar group or that have experienced higher levels of education, who tend to have a higher valuation for the Supporting services.

In summary the outline of this study demonstrates that different ecosystem services are of unequal importance from an anthropocentric point of view. Therefore, different measures should be taken into account when judging forest value. Such measures might provide ecologists important weights of different ecosystem functions to assess the relative importance of trade-offs between such ecosystem services when assessing the whole ecosystem multifunctionality, especially with respect to political consulting. In addition, this study shows that people from the rural areas of southeastern China still need more education to raise and improve awareness towards the significance of forest biodiversity.

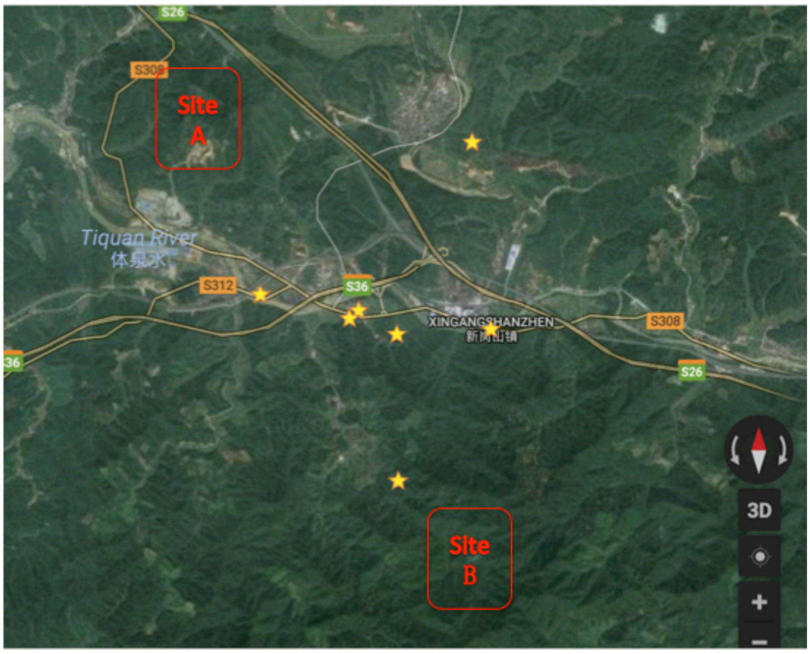


Fig. 1 Map shows the position of the villages (represented by the stars) that close to BEF-China experimental sites (site A and site B are shown here).

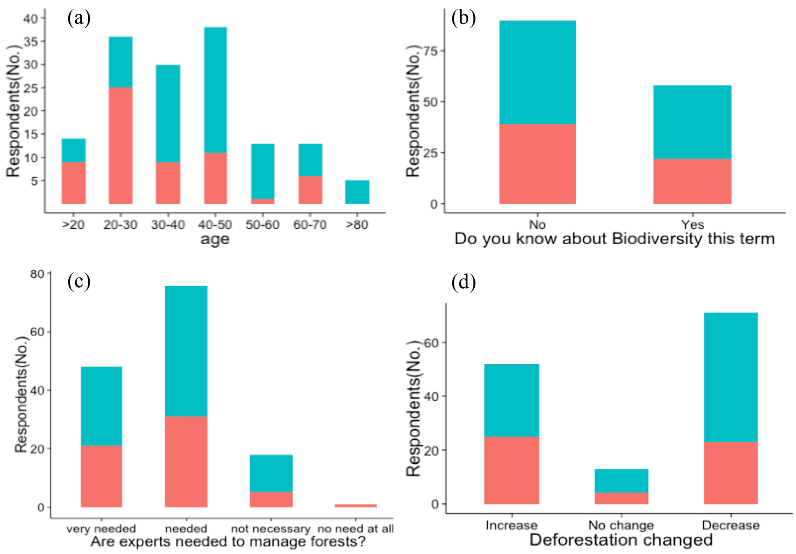


Fig. 2 General information about the subjects (a), whether they ever heard about the biodiversity term (b), and their attitude towards forests (c, d). Red color represents female, while light blue represents male subject.

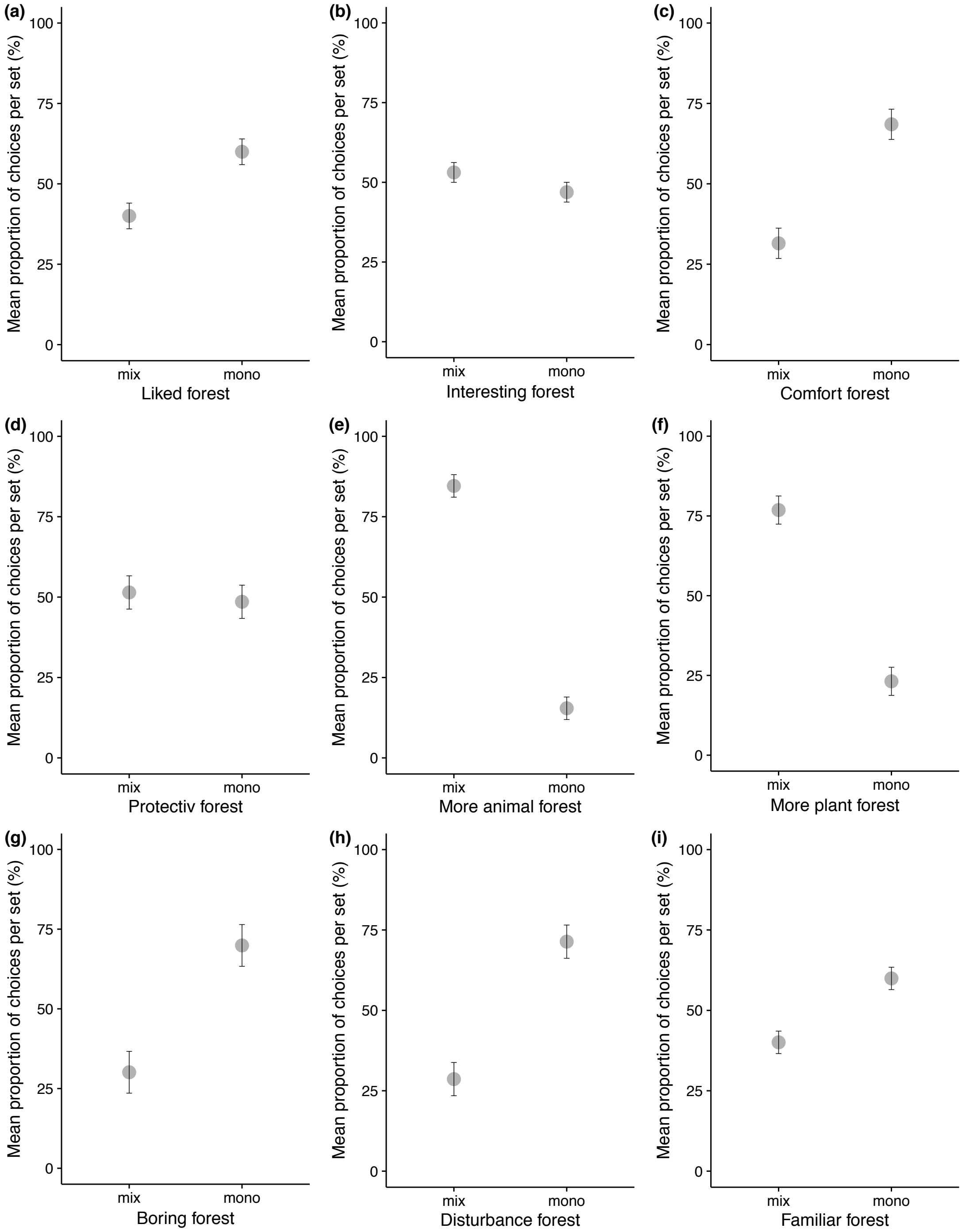


Fig. 3. Attitudes towards forest diversity. In choice task, 62 female and 88 male people pointed out the forest they liked most (a), thought to be interesting (b), comforting (c), worth protecting (d), richest in animal species (e), richest in plant species (f), boring (g), disturbed (h) and familiar (i). According to the question, each person chose one picture from the four pictures (two monocultures, two species-rich forests) in one set, which was randomly chosen from 10 picture sets.

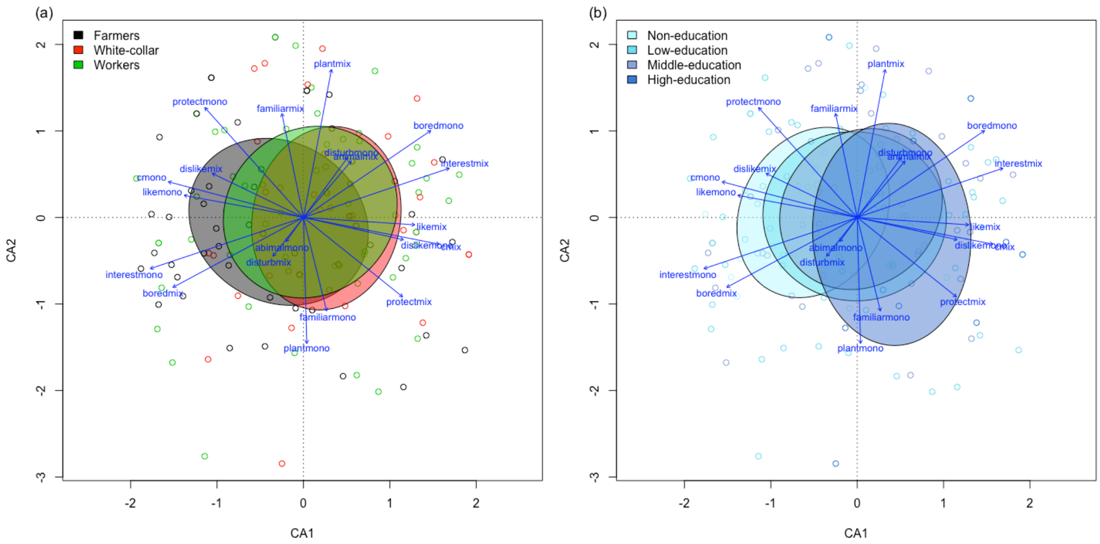


Fig. 4. Canonical correspondence analysis (CCA) diagram with subjects (dots) and attitude towards the mixture or monoculture forests (arrows). It shows the relationships between the educational level (a) or professions (b) and attitude towards forest diversity. Ellipsoids represent the projected 2-dimensional mean (i.e. centroid) and standard deviation of the subjects categorized into the groups depicted in the figure legend. Ordination function CCA in vegan package was used for analysis. Only the axes 1 and 2 are shown. Eigenvalues: axis 1 = 0.022, axis 2 = 0.011 with cumulative proportion of explained variance 33.11%. See Fig. 3 legend for abbreviations of people's attitude towards forest diversity.

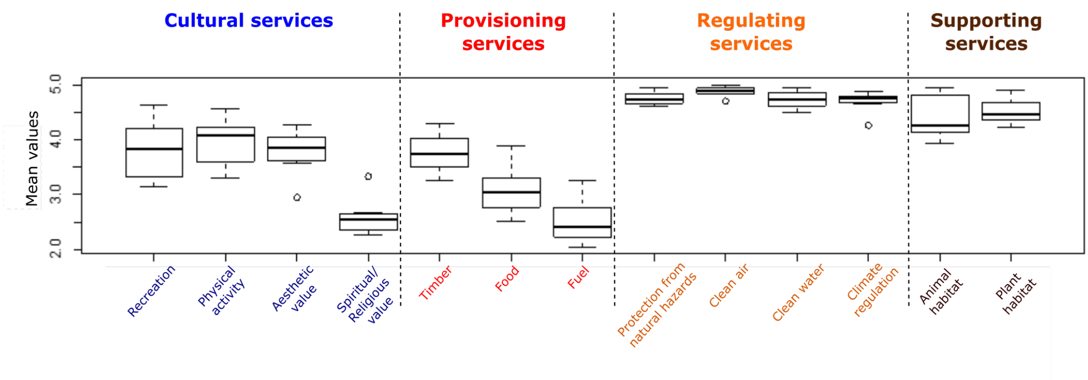


Fig. 5. Self-reported importance values assigned to forest ecosystem services. People were asked to give a value from 1 to 5 to assess different ecosystem services importance. Mean values were derived from raw data based on categorical measures from a five-step scale: 1 = unimportant, 2 = rather unimportant, 3 = neither/nor, 4 = rather important, 5 = important. Cultural services (blue) include if forests are perceived as place for recreation, place for physical activity, of aesthetic or of spiritual/religious value. Provisioning services (red) include whether forests are important for the production of timber, food, (e.g. mushrooms) and/or providing fuel. Regulating services (orange) include how forests are perceived as protection against natural hazards (e.g. erosion), produces clean air and/or clean water and are important in climate regulation. Supporting services (brown) comprise whether the forest is perceived as an important habitat for animals and/or plants.

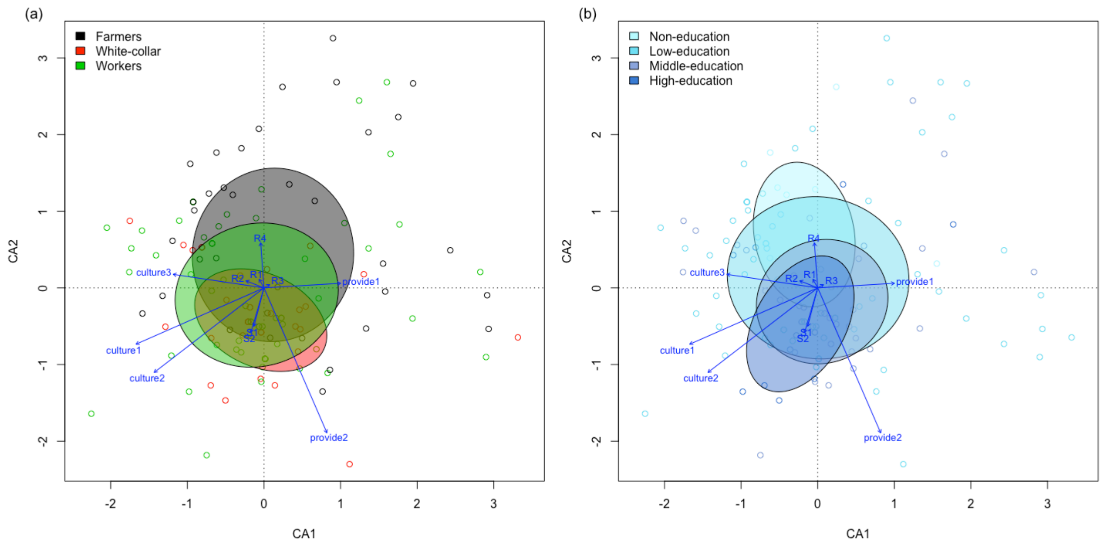


Fig. 6. Canonical correspondence analysis (CCA) diagram shows the relationships between the education level (a) or professions (b) and attitude towards ecosystem services (blue arrows). Ellipsoids represent the projected 2-dimensional mean (i.e. centroid) and standard deviation of the subjects categorized into the groups depicted in the figure legend. Ordination function CCA in vegan package was used for analysis. Only the axes 1 and 2 were shown here. Eigenvalues: axis 1 = 0.017, axis 2 = 0.013 with cumulative proportion of explained value 27.19% and 47.18% respectively. Abbreviations of ecosystem services: culture 1 = recreational value; culture 2 = physical use; culture 3 = aesthetic value; culture 4 = spiritual value; provide 1 = timber production; provide 2 = food production; provide 3 = fuel provisioning; R1 = protection against natural hazards; R2 = production of clean air; R3 = production of clean water; R4 = climate regulation; S1 = habitat for animal species; S2 = habitat for plant species.

Appendix 2 Questionnaire

BEF-China 调查问卷 号码：_______ 地点：_________ 时间：______________________

性别	年龄	文化水平	职业	家庭人口数	学生人口数	山地面积	每亩树木产量
						亩	立方米/方

砍伐树木数量		砍伐的物种	
知道 BEF-China 项目吗?	(知为 1，不知为 0)	在 BEF 的工作年限	

A1. 您觉得种植单种林（杉木林）好还是多物种混交林好？为什么？

☐1 单种林 ☐2 杂交林； 原因:_____

A2. 种植单一树种有没有发生过什么严重灾害造成严重的损失？（比如有没有虫灾、旱灾？）

A3. 种树吗？植树有什么技术吗？

种植什么物种？

杀虫剂、肥料种类，使用量？

从哪获得的种子或幼苗？

A4 您觉得新岗山地区生态系统情况如何？

☐1 非常好; ☐2 好; ☐3 一般; ☐4 不好; ☐5 破坏非常严重

A5 您觉得山地面积这十年来有什么变化？

☐1 增加了; ☐2 没变; ☐3 减少了; 具体变化了多少_________________________

A6 您觉得森林砍伐近 10 年来有什么变化？

☐1 增加了; ☐2 没变; ☐3 减少了; 具体变化了多少_________________________

A7 树木物种价格及近十年变化（升高为 1、不变为 0、降低为 2）石栎： 香樟：

杉木： 马尾松： 荷木： 甜槠： 枫木： 其他：

A8 您觉得森林需要有专业人员管理和维护吗？

☐1 非常需要； ☐2 需要； ☐3 不需要； ☐4 完全不用

A9 如果新研究表明，种植更多样的物种能使树长得更好，但需要花较长的时间，您愿意尝试吗？

☐1 非常愿意； ☐2 愿意； ☐3 不太愿意； ☐4 完全不愿意

A10. 森林保护的政策近十年来有什么变化吗？

A11 你能使用智能手机上微信，查收资料吗？ ☐1 能； ☐2 不能

愿意用手机来收取生物多样性知识吗？ ☐1 愿意； ☐2 不愿意

B1 根据你的观点，选择照片来回答问题. 图片编号:_________（照片从左到右为 1、2、3、4）

…1 你最喜欢的？（ ） …2 你最熟悉的？（ ） …3 有最多的动物种类生活其中？（ ）

…4 被最严重耕作过的？（ ） …5 最有价值，最值得保护？（ ） …6 你最不喜欢的？（ ）

…7 有最多的植物种类?（ ） …8 是最单调乏味的？（ ） …9 最有趣的？（ ） ..10 最让人感到舒服的？（ ）

B2 您知道生物多样性这个概念吗？ ☐1 知道；☐2 不知道

如果知道，从哪听说的？☐1 报纸; ☐2 杂志; ☐3 电视; ☐4 网络; ☐5 收音机; ☐6 学校; 7 其他__________

如果知道，对生物多样性的定义包括以下哪个选项？(多选题)

☐1 植物的多样性；☐2 动物的多样性；☐3 遗传的多样性

☐4 自然环境的多样性；☐5 植物与动物的关系的多样性；☐6 有机食物的种类多样性

B3 您对生物多样性相关的问题感兴趣吗？

☐1 非常感兴趣; ☐2 感兴趣; ☐3 一般; ☐4 不感兴趣; ☐5 不在乎

B4 生物的多样性是植物、动物多样性（品种数量），遗传多样性以及环境多样性的总称。

您认为生物多样性跟您日常生活有关系吗?

□1 非常相关；□2 相关；□3 一般；□4 不相关；□5 完全不相关

B5 您认为世界上有多少植物物种?

□A.>1 亿; □B.千万；□C.百万；□D.几十万；□E.几万；□F.几千； ___________

中国有多少植物物种？□A.千万; □B.百万; □C.几十万; □D.几万; □E.几千; ______

新岗山一亩的山林里有多少植物物种？□A. >1000; □B.100-1000; □C.50-100; □D.10-50; □E.＜10

B6 您觉得新岗山的生物多样性与 10 年前相比有变化吗? □1 增加; □2 不变; □3 减少

引起生物多样性变化原因有哪些？（多选）

□1.山地面积减少；□2.入侵物种; □3.气候变化;

□4.工业发展，破坏环境; □5.森林砍伐; □6.乱扔垃圾，污染环境；□7.打猎; □8 其他________________

B7 您觉得当地有哪些动植物需要被保护?

B8 您愿意做哪些行动，来保护新岗山的生物多样性?

□1 不乱扔垃圾；□2 种树；□3 不盗伐滥伐；□4 不打猎；□5 举报威胁环境的行为； 6 其他_____

B9 您认为自己的植物知识跟一般大众比起来要更丰富吗?

□1 非常丰富（专业背景知识）；□2 比较丰富；□3 一般；□4 不好；□5 非常不好

B10 如果你想走进大自然,以下哪个地方是你最想去的?

□1 湖泊; □2 森林; □3 山峰; □4 江河; □5 草原

B11 你平均多久走进一次森林?

□ 1 每天; □2 一天到一周; □3 一周到一月; □4 一月到一季; □5 大于一季

B12 你选择去森林的主要原因是什么?______________________________

B13 在森林所起到的以下功能中,对你来讲其重要程度是?（请在括号中写下对应重要程度数字）

森林功能	重要程度	重要 (5)	比较重要 (4)	不确定 (3)	一般不重要 (2)	不重要 (1)

[A] 供应功能

生产木材 1 …( )

生产食品(例如蘑菇)2… ( )

生产燃料(例如薪炭材)3… ( )

[B] 调控功能

防御自然灾害(例如水土流失)1… ( )

产生清洁空气(提高空气质量) 2… ( )

产生清洁水 3 … ( )

调节气候 4 … ( )

[C]文化方面

是可以休闲的地方 1… ( )

是可以锻炼身体的地方 2… ( )

具有美学价值 3… ( )

具有宗教/精神价值 4… ( )

[D] 支持方面

是动物栖息之地 1… ( )

是植物生长之地 (树木以外的植物)2… ( )

B14 你对下列问题是何观点?

	同意 (5)	比较同意 (4)	不确定 (3)	比较不同意 (2)	不同意 (1)
a 我国拥有足够的森林	□	□	□	□	□
b 我国森林受到太多人工管理	□	□	□	□	□
c 森林应当向每个人开放	□	□	□	□	□
d 采集森林产品应被限制	□	□	□	□	□
e 我国的森林保护区很少	□	□	□	□	□

感谢您的参与！祝您工作顺利，生活愉快！

Appendix 3 Newsletters

IDP BRIDGES*News* No 2, 2015

Diversity and primary productivity in subtropical forests—fixing carbon to mitigate climate change

This project will explore whether more diverse forests can take up more carbon dioxide from the atmosphere and thus reduce global warming.

YUANYUAN HUANG

Developing better forest biodiversity management strategies helps to optimize ecosystem services provided by forests, in particular carbon storage and erosion control.

I measure tree growth as a function of different aspects of tree diversity a) in comparative study plots varying in successional stage and tree species richness and b) in experimental plots varying in tree species richness and composition. More than 500 plots have already been set up in south-east China. My main task will be synthesizing my own and other data from these plots to predict ecosystem services provided by forests of different tree diversity and scaling up from plot to local and regional level. Based on the field measurements, structured interviews, discussions with forest companies, local authorities and forest visitors, I will develop forest biodiversity management strategies and supply scenarios and guidelines for forest plantation in subtropical areas in China and elsewhere.

Secondment

Yuanyuan will spend three months at the **Institute of Botany of the Chinese Academy of Sciences (IBCAS)**. She has conducted field measurements of tree growth in south-east China in collaboration with the local forest company and farmers. She also has been disseminating and discussing her work with forest managers and government officials. She will soon organize guided tours and interviews with forest visitors with explanatory plates and leaflets.

In the end, she will develop management scenarios with researchers involved in carbon mapping and climate mitigation for China.

About the organization

The Institute of Botany of the Chinese Academy of Sciences (IBCAS) is one of the oldest comprehensive research institutions in China, which has led the development of plant science in China since its establishment in 1928. The institute has received three first-level National Natural Science Awards, as well as more than 160 awards at the national and provincial level. With a focus on integrative plant biology, IBCAS conducts innovative research at the molecular, cellular, physiological, ecological and landscape levels, and develops applications to benefit agriculture and the environment.

http://english.ib.cas.cn/

Associate partner

Prof. Keping Ma, IBCAS, China

Yuanyuan Huang
University of Zurich, Institute of Evolutionary Biology and Environmental Studies
Supervisor: Prof. Bernhard Schmid

CASE STUDY 4

BIODIVERSITY CONSERVATION THROUGH COFFEE AGROFORESTRY

Coffee is a major economic source of income in the Kodagu district of the Western Ghats, whereby coffee agroforestry systems represent the majority of remaining biodiversity outside the protected forest. The area of protected forest has declined by 50% over the last 40 years. A development of coffee intensification and shade tree homogenization has taken place due to many factors. One main factor that has been identified is the law implemented by the ministry of forestry. It prohibits the logging of native tree species which results in farmer's preference for exotic tree species. This preference originates from the profitability of selling the timber of the fast growing exotic species. Previous research has struggled with the complexity of the problem at hand, consisting of how to maintain or even increase the biodiversity at a landscape scale. This is due to the interconnectedness of a multitude of system components and the contrasting perspectives, objectives and needs of the different stakeholders involved. The problem has been identified as being a wicked problem since interventions have always been accompanied by negative side-effects. Moreover, multiple objectives and perceptions have hindered successful implementation of suggested measures. Erratic changes of conditional factors on different scales such as the volatility of coffee and timber prices, climate variability and climate change but also unintended consequences of intervention measures result in a need for continuous adaptation. ... In order to achieve a more resilient ecosystem and maintain/increase farmers' livelihoods, we propose co-producing locally adapted sustainable agricultural practices together with farmers, taking into account the institutional context. These objectives are based on the following values: i) biodiversity provides a resilient and stable ecosystem over the long-term (sustainability) and ii) human rights, e.g. equal availability to resources, work, respect, economic welfare, etc. … There are several stakeholders, such as the NGO (ATREE) and the forestry-ministry, in the position of making decisions about the needed human, financial, natural, and political resources. It is of great importance that the decision makers are ideally independent of the decision environment. ... It is crucial to consider any possible risks and side-effects caused by the project implementation to assure legitimacy. This is done by considering potential victims (e.g. current generation of farmers and their families, parts of the ecosystem or the government budget), negative impacts that should be avoided (e.g. increased deforestation of primary forest or human-wildlife conflict) and the different world-views of the involved actors.

Extract of the case study work from Yuanyuan Huang, Nestor Pöll, Laura Damerius and Eric Rahn
Case study facilitator: Claude Garcia, ETH Zurich, ForDev

Links

www.fordev.ethz.ch/research/research-and-thesis-projects/south-asia/landscape-transition--impacts-on-pollination-service-in-the-west.html

www.blackbazacoffee.com

IDP BRIDGES*News* No 4, 2016

Secondment Report

Yuanyuan Huang collecting data

About IBCAS

The Institute of Botany of the Chinese Academy of Sciences (IBCAS) is one of the oldest comprehensive research institutions in China, which has led the development of plant science in China since its establishment in 1928. The institute has received three first-level National Natural Science Awards and more than 160 awards at the national and provincial level. With a focus on integrative plant biology, IBCAS conducts innovative research at the molecular, cellular, physiological, ecological and landscape levels and develops applications to benefit agriculture and the environment.

http://english.ib.cas.cn/

Fixing carbon to mitigate climate change

YUANYUAN HUANG

My project explores whether more diverse forests can take up more carbon dioxide from the atmosphere and thus reduce global warming. We aim to develop a better forest management strategy and to enhance the public awareness of the protection of forest species. During my secondment I had the opportunity to cooperate with my associated partner, Prof. Keping Ma, who initiated biodiversity research in China in the early 1990s and is an expert in digitalization of biodiversity information. Together with colleagues from China, Germany and Switzerland he built up the research platform BEF-China, one of the largest Biodiversity–Ecosystem Functioning research platforms in the world, in Jiangxi province in south-east China. I took tree inventories there to find out the best diversity of the tree species that maximizes productivity and thus carbon uptake. During the same time, I set up a micro-channel public platform through which people can receive biodiversity and forest ecosystem related information with cellphone. We also did some teaching in local primary school, contributing to children's education of forest conservation.

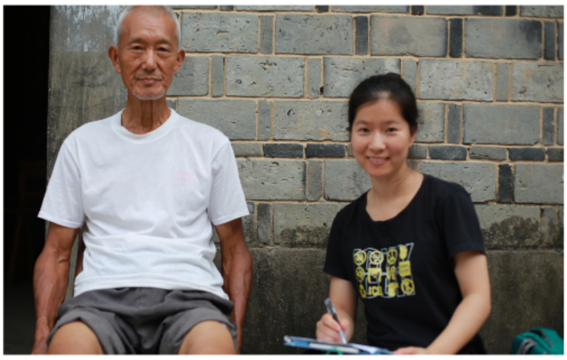
The BEF-China platform is located in a quite area surrounded by mountains, far away from big cities. Old generations of local people are very knowledgeable about forest ecology. They have good experience about where and how to grow particular tree species. Using questionnaires and interviews with local farmers, forest managers and government officials, I assessed attitudes towards forest diversity and ecosystem services as well as knowledge about forest management.

"Now we forbid cutting broad-leaf tree species. The economic trees will strictly be managed according to stand age..."

...the chairman of the board of the forest company in the town told us.

Cooperation and teamwork were very important for my secondment. My colleagues Bo Yang and Xiaojuan Liu, both coordinators of the BEF-China project from Prof. Ma's group, were very helpful. Besides gaining skills of inventorying trees, interviewing people and digitalization biodiversity information, the biggest benefit for me was to communicate with different people whom I would never have met and talked to otherwise. I learned to look at the world in different perspectives, which broadened my research ideas.

Back here in Zurich, I am analyzing the data collected during the secondment and building a forest-management model. The interviewing experience benefits my future social-science work. My experience of the digitalization of biodiversity information makes it easier for me to present scientific research to the public. The platform I built can help to increase people's awareness of biodiversity, as well as increase cooperation. The memories of my secondment will remain in my mind and brighten my way.



Interview with local farmer

English course in local primary school about forest ecosystem services

Tree inventory places in Jiangxi province in southeast China

IDP BRIDGES*News* No 6, 2017

Fellows Report

Interview with local famer in Jiangxi province in southeast China
© Yuanyuan Huang

Collaborators
Yuanyaun Huang[1], Bernhard Schmid[1], Pascal Niklaus[1], Ma Keping[2]

[1] University of Zurich, Department of Evolutionary Biology and Environmental Studies, Switzerland
[2] Institute of Botany of the Chinese Academy of Sciences, China

Fixing carbon in subtropical forest to mitigate climate change: How to transfer the knowledge to farmers

Yuanyuan Huang

Forest ecosystems contain the majority of the carbon stored in terrestrial ecosystems, and play an important role in helping mitigate climate change. A central question in biodiversity research is how experimental manipulations of plant diversity affect primary productivity including carbon storage. Grassland experiments have shown a positive relationship between the two variables, but it is not clear if the same holds for forests.

We tried to understand whether more diverse forests provide more forest ecosystem services. With observational studies, we found that biodiversity can promote tree growth in natural forest. By monitoring tree growth of around 13.000 trees in 512 plots with six biodiversity levels (1, 2, 4, 8, 16 or 24 species) for four years (2013–2016) in a field-manipulated experiment, we discovered that more diverse plantations during the initial 7 years of growth accumulated more biomass, and this positive diversity effect increased with time. It turned out pathogens and herbivores inhibited productivity more in low than in high diversity. Thus, it is important to take species' richness into account in afforestation. Our results can be directly linked to on-going assessments that sup-port forest policy design, strengthening the science - policy interface for the conservation and sustainable development.
We carried out questionnaire surveys and interviews with stakeholders in five villages near the field site to obtain a good understanding of their attitudes toward forest ecosystem and biodiversity. We also built up a micro-blog, through which people can receive information about «biodiversity and forest ecosystem functioning» on their mobile phones. However, it is not easy to successfully integrate decision makers into the project without any immediate practical profits for them. This causes some difficulties to translate the scientific data into actual management decisions.

—
Presentations
Poster at the PSC PhD Symposium «Unlocking the Potential of Diversity», 2015
Talk at the Annual Meeting of the Ecological Society of America, 2016
A talk «Resilience of tropical ecosystems – Future challenges and opportunities» at Annual Conference of the Society for Tropical Ecology, 2015
A poster at PopBio, 2015

—
PSC Teacher Workshop
«Plant ecophysiology» University of Berne, 2016

—
School class Workshop
«I love forest» for primary school in the BEF-China experimental area, Xingangshan, JiangXi province China, 2014

—
Web and social media
Micro-blog «Biodiversity and ecosystem functioning» with the platform of Wechat on cellphone (Wechat ID: BEF-China)

https://befchina.wordpress.com/

Appendix 4 Posters

Resources and enemies, which have bigger influence on the biodiversity-ecosystem functioning relationship in subtropical forest?

Yuanyuan Huang; Bernhard Schmid; Pascal Niklaus
Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

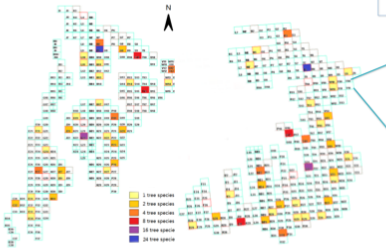
INTRODUCTION

Aboveground primary productivity is one of the most important ecosystem functions in the forest, and has been found increasing with biodiversity in many studies. Lots of the experiments have been done in the grassland to identify the complementary effect, selection effect and soil microbes' effect on this relationship. However, there is little knowledge about the mechanisms in the subtropical forest. Here, we conducted an experiment in a large biodiversity-ecosystem functioning experiment platform in JiangXi Province, China (BEF-China). Our study contribute to the explanation of the biodiversity-ecosystem functioning relationship's underlying mechanism in subtropical forest.

STUDY DESIGN

Location: JiangXi Province, China (dark green area)

Bruelheide, H., et al. (2011), Ecological Monographs



Site A set up in 2009

Site B set up in 2010

Experimental plots: colored squares, 32 plots per site

Treatments

Biotic impacts (Density-dependent)

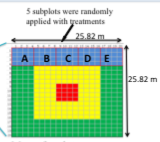
1. F: fungicide (Pathogen exclusion)
2. I: insecticide(Herbivore exclusion)

Resource-niche based complimentary

3. N: NW no weeding (i.e. admitting all types of weeds)
4. P: Phosphorus fertilizer

5. C: Control (ie. weeding)

5 subplots were randomly applied with treatments



Map of a plot

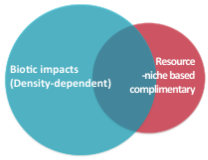
Diversity treatment

- ➢6 diversity levels: 1, 2, 4, 8, 16, 24
- ➢Species pool: 40 tree species
- ➢Random extinction

HYPOTHESES

- H1: Tree biomass increases with diversity.
- H2: Biodiversity effect results from a reduced pressure from host-specific predators and pathogens, and high resource-based niche complementarity in high diversity forest.
- H3: Effect from host-specific predators and pathogens is bigger than resource-based niche complementarity effect.

Higher divrersity → less host-specific pathogens and herbivores
Higher diversity → higher resource use efficiency



Modification of biotic interactions and resource supply (BEFmod)

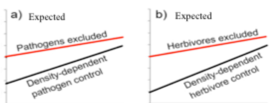
DATE ANALYSIS

Mixed-effect model (Asreml in R)

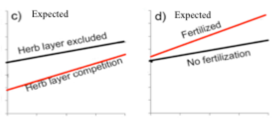
Basal diameter ~ site+species identity + (logSP+DIV)*treatment, random=~plot+plot : subplot

	Df	denDF	F value	P value
(Intercept)	1	39.2	586.7	< 0.001***
site	1	39.2	36.99	< 0.001***
species identity	34	768.3	32.78	< 0.001***
logSP	1	41.8	11.41	0.002**
DIV	4	42.5	0.22	0.93
treatment	4	197.5	1.5	0.20
logSP:treatment	4	278.3	1.21	0.31
DIV:treatment	16	345.4	1.86	0.02*

RESULTS



Slopes are smaller than the *Control*
Enemies: √



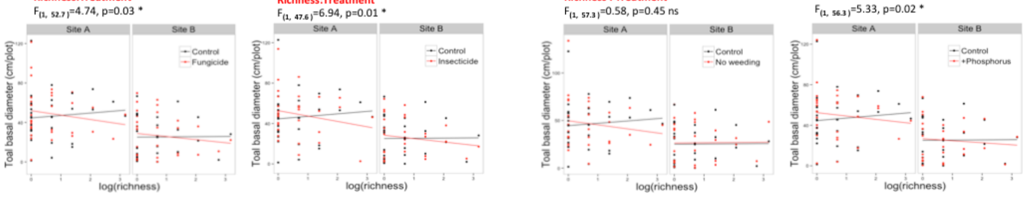
Slopes are not steeper than the *Control*
Resources: ×

Richness:Treatment
$F_{(1,\ 52.7)}$=4.74, p=0.03 *

Richness:Treatment
$F_{(1,\ 47.6)}$=6.94, p=0.01 *

Richness : Treatment
$F_{(1,\ 57.3)}$=0.58, p=0.45 ns

Richness : Treatment
$F_{(1,\ 56.3)}$=5.33, p=0.02 *



Conclusions

- **Positive main diversity effect, and this effect increases with time.**
- **Herbivores and pathogens do has an effect on this positive relationship as we expected, but not for the resource-based niche complementarity effect.**
- **Enemies may play a more important role in this subtropical forest than resources.**

Acknowledgement: This study was financed by the German Research Foundation DFG and Zurich-Basel plant science center.

BEF-China web: http://www.bef-china.de/index.php/en/
Contact: yuanyuan.huang@ieu.uzh.ch

Universität Zürich[UZH] DFG Deutsche Forschungsgemeinschaft Zurich-Basel Plant Science Center FOR 891 BEF China

Biodiversity increases wood production in a forest experiment

Disentangling mechanisms across time

We explored how the effects of tree and shrub diversity on forest production change across temporal and spatial scales

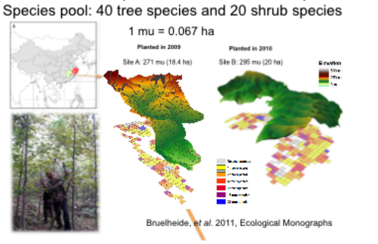
Yuanyuan Huang; Yuxin Chen; Pascal A. Niklaus; Bernhard Schmid
Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

Conclusions

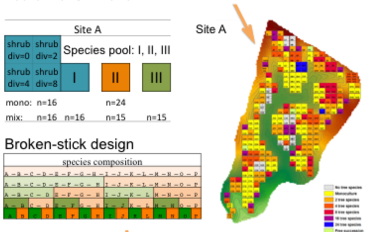
1. First large-scale demonstration of a strong, positive scale-independent diversity-productivity relationship, which increases over time in a manipulated forest experiment.
2. Our findings highlight the importance of the understory shrub species richness and their effect on tree community productivity.
3. Our experiment matched to local situations in China, as one of the biggest reforestation nations in the world. Our results will provide a practical solution to conserve and manage forest ecosystem services.

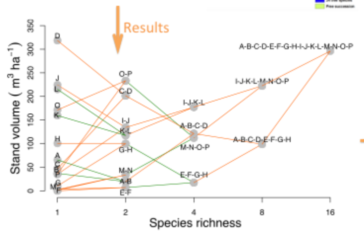
How

6 levels of tree species richness:1, 2, 4, 8, 16, 24 species
4 levels of shrub species richness: 0, 2, 4, 8 species
Species pool: 40 tree species and 20 shrub species



Measured 6,336 trees in 140 small plots (1 mu) and 64 large plots (4 mu) , i.e. 396 1-mu (sub)plots in total
Years: 2013 – 2016





Note: Orange lines represent overyielding; green lines represent underyielding

What we found

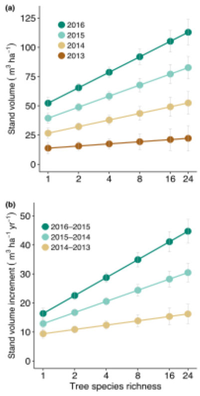


Figure 1 | Positive effects of tree species richness increase with time. Points, error bars and lines are predicted from mixed-effects models.

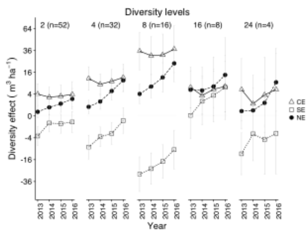


Figure 3 | Diversity effects across time in mixtures of different richness levels.
NE: Net effect
CE: complementarity effect
SE: selection effect
Positive net effect increased through time ($F_{1, 74.5}$ = 18.30, $P < 0.001$, diversity effects were square-root transformed before conducting the ANVOA).

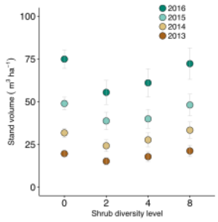


Figure 2 | Effects of shrub diversity on tree stand volume. Understory shrubs had a negative effect on tree stand volume, but this negative effect was attenuated by increasing shrub species richness.

Table 1 | Summary statistics from the mixed-effects models for effects of shrub species richness and plot size on tree stand volume.

Source of variation	df	ddf	*F*	*P*
site	1	44.00	13.27	<0.001
logSR	1	43.20	4.56	0.038
shrub v.s. non-shrub	1	247.80	6.15	0.014
plot.size	1	116.30	0.22	0.643
lgshrub	1	188.00	5.10	0.025
year	1	46.60	85.42	<0.001
logSR × shrub v.s. non-shrub	1	247.80	0.96	0.330
logSR × plot.size	1	116.30	0.25	0.615
logSR × lgshrub	1	188.00	0.27	0.602
logSR × year	1	46.60	7.45	0.009
shrub v.s. nun-shrub × year	1	249.80	9.45	0.002
plot.size × year	1	120.60	0.01	0.941
lgshrub × year	1	190.00	3.25	0.073

Note:
Random terms: species composition, plot, subplot and their interactions with year.
comm = species composition in the plot;
logSR = $\log_2$(tree species richness);
lgshrub = $\log_2$(shrub species richness)

Why

- Forest ecosystems contain around two thirds of all terrestrial species, but currently suffer the danger of species loss.
- Given the global interest in mitigating climate warming, tree species loss may lower the capacity of forests to absorb carbon dioxide from the atmosphere, especially in growing forests.
- Challenges: long life span of trees; complicated vertical structures; large area for forest stand establishment.
- There is a large knowledge gap about how diversity will affect ecosystem functions across temporal and spatial scales in diverse forests.

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